

ASSESSING THE DEMOGRAPHIC AND GENETIC CONTRIBUTIONS OF PRECOICIAL
MALES IN A NATURALLY SPAWNING POPULATION OF COHO SALMON

By

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ABSTRACT

Despite the importance of alternative life history strategies to population productivity, little is known about the mating structure of precocial ('jack') males in Pacific salmon. The number of successful matings obtained by jacks in the wild is not well characterized and the impact of including or excluding jacks in the management of Pacific salmon populations is unknown. This study aims to fill knowledge gaps in the understanding of jack life history by 1) determining the typical contribution of jacks to the next generation in a natural mating population; and 2) estimating the impact of jacks on genetic diversity. The study capitalizes upon 11 years of demographic and genetic data from a naturally spawning population of Coho Salmon from Auke Creek, in Juneau, Alaska. Individuals returning over this time period (~8,000 individuals) were genotyped at ~250 single-nucleotide polymorphism (SNP) loci. Using these genotypes, we quantified the adult-to-adult reproductive success of different male types using parentage analysis for each of seven return years and compared genetic and demographic estimates of effective population size. We demonstrated that although jacks were less successful than full-size males on a per individual basis, they contributed substantially to the population and influenced population and evolutionary dynamics.

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GENERAL INTRODUCTION

Diversity of life history strategies within a species can contribute to population viability. Per the portfolio effect, reductions in population biocomplexity decrease existing population resilience (Schindler et al. 2010). A useful way to examine trends in genetic drift and inbreeding and to predict what will happen in future generations is to monitor effective population size (N_e), which is inversely related to the loss of genetic diversity. It is known that the presence of different life history forms can increase N_e in various species, like Atlantic Salmon *Salmo salar* and Brown Trout *Salmo trutta* (Garcia-Vazquez et al. 2001). Therefore, understanding the contribution of life history diversity to genetic diversity is essential for monitoring species of conservation concern.

Pacific salmon (*Oncorhynchus spp.*) demonstrate an abundance of life history variation, and many populations are of great conservation concern. Pacific salmon are anadromous, meaning that they are born in freshwater, migrate to the ocean to grow and mature, then return to freshwater to spawn. They are also semelparous, meaning they only have one reproductive event in their lifetime. During spawning, females dig a nest ('redd'), and their eggs are externally fertilized by a male at the time they are laid. Within and among species of Pacific salmon, there is variation in out-migration timing, age at out-migration, return timing, and many other traits. Two important axes of life history variation within species are age and size at maturity. Fish of different ages and sizes typically have different natural and fisheries-induced mortality rates and reproductive output (e.g., Berejikian et al. 2010; Kendall and Quinn 2013; Ohlberger et al. 2020).

One common alternative life history form related to age and size at maturity is precocial males, known as 'jacks' in Pacific salmon. Jacks are males that mature at a smaller size than full-size males and spend less time at sea before maturing. To achieve mating, jacks use sneaking tactics to gain access to females and their redds as opposed to direct competition for mates, which is common among the full-size males (Gross 1985). The difference between jacks and full-size males is that jacks reach the threshold at which sexual maturation occurs at a smaller size and typically younger age than full size males. This threshold is related to size, growth rate, and energy stored (Aubin-Horth and Dodson 2004; Piché et al. 2008) and is influenced by

environmental (Bilton et al. 1982; Vøllestad et al. 2004) and genetic factors (Iwamoto et al. 1984; Hankin et al. 1993; Heath 1994; see also McKinney et al. 2021).

The small size of jacks reduces their value to commercial fisheries and makes them difficult to count in surveys of natural populations. Consequently, jacks are not always monitored and their contribution to the population is assumed negligible. Even though this assumption is common, there is limited evidence to support it. The amount of returning adult offspring produced by precocial males has not been well researched, and their reproductive success relative to full-size males is not well characterized. Research has indicated that jacks can be successful at fertilizing eggs and producing offspring that survive to the fry stage, but their success can range widely (Foote et al. 1997; Berejikian et al. 2010). Additionally, the contribution of jacks to the maintenance of genetic diversity is not well known. There is little information on the contribution of precocial males to N_e in natural populations of Pacific salmon. This knowledge gap is problematic and surprising given that jacks can make up anywhere from <1 to >50% of the male brood year returns (e.g., Sockeye Salmon *Oncorhynchus nerka*, Quinn et al. 2001; Coho Salmon *Oncorhynchus kisutch*, this study).

Insight on jack mating success and contribution to N_e would be valuable for conservation programs, including hatcheries. Hatcheries are used to enhance harvest and/or compensate for habitat loss; however, genetic modification of wild populations when hatchery fish are integrated (either on purpose or by accident) into wild populations is a concern. Wild populations are locally adapted, and hatchery fish often have reduced survival and reproductive success in the wild (McGinnity et al. 2003; Araki et al. 2007; Koch and Narum 2021), so when hatchery fish interbreed with wild fish, the genetic composition of the next generation of wild fish is altered in a way that can lower their survival and reproductive success. There are different outcomes under different scenarios and the outcome depends on how well/poorly adapted hatchery fish are and how many hatchery fish breed with wild fish (Koch and Narum 2021). To avoid altering the genetic composition and reducing the fitness of wild populations, integrated hatcheries attempt to limit changes to the genetic composition of hatchery populations. Despite the objective of limiting genetic changes to hatchery populations and avoiding selective breeding, hatcheries

often engage in practices that may not mimic natural mating strategies, such as excluding jacks from the broodstock. The impact of this divergence from natural mating structure is unknown.

In this thesis, I examined two questions regarding intense selection against jacks: 1) what is the typical reproductive contribution of jacks to the next generation in natural mating populations; and 2) what is the contribution of jacks to the maintenance of genetic diversity? To address these objectives, I utilized a decade of demographic and genetic data from ~8,000 Auke Creek Coho Salmon sampled from 2009 to 2019. At a two-way weir operated by National Oceanic and Atmospheric Administration (NOAA), adult salmon are intercepted in the creek on their way to spawn. Each fish is transported over the weir manually, allowing every returning fish to be sampled. This dataset is uniquely valuable due to the fact that I have access to nearly every returning adult Coho Salmon during this period, which allowed me to use the genetic samples to pair offspring and parents and leverage parentage analysis to answer our questions of reproductive success and genetic diversity. This approach is useful for determining reproductive success and has been applied widely to Pacific salmon elsewhere (e.g., McLean et al. 2008; Thériault et al 2011). Most studies are limited to using only proportions of populations, because of the difficulty in sampling all individuals. This study offers a unique opportunity to fill gaps in our knowledge about an alternative life history tactic relevant to the conservation of Pacific salmon.

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CHAPTER 1: REPRODUCTIVE SUCCESS OF PRECOICIAL AND FULL-SIZE MALES IN A WILD COHO SALMON POPULATION¹

1.1. Abstract

Despite the wealth of research on Pacific salmon *Oncorhynchus* spp. life histories there is limited information on the lifetime reproductive success of precocial males (“jacks”). Over half of the returning male spawners can be jacks in some populations and some years, so it is crucial to understand their contribution to population productivity. We quantified adult-to-adult reproductive success (RS) of jacks, of which estimates are rare, and their relative reproductive success (RRS) compared to full-size males in a wild population of Coho Salmon in the Auke Creek watershed, Juneau, AK. We used genetic data from all individuals (~8,000) returning to spawn over a decade (2009–2019) to conduct parentage analysis and calculate RS of individuals. The average adult-to-adult RS of jacks (mean=0.7 & SD=1.9) was less than that of full-size males (mean=1.1 & SD=3.3). Jack RRS was consistently below 1.0 but ranged widely (0.23 to 0.96). Despite their lower average success, jacks contributed substantially to the population by fathering 23% of the total returning adult offspring (1,033 out of 4,456) produced between 2009 and 2015. Our results demonstrate that jacks can affect evolutionary and population dynamics and they are relevant to the conservation and management of Pacific salmon.

¹ King, E., D.A. Tallmon, S. Vulstek, and M.V. McPhee. Reproductive success of precocial and full-size males in a wild Coho Salmon population. Manuscript in preparation for Transactions of the American Fisheries Society. Journal subject to change.

1.2. Introduction

In Pacific salmon *Oncorhynchus* spp., extensive variation in life history strategies and traits has enabled their wide-ranging distribution and persistence for millions of years. Diversity in life history types is beneficial for population resilience (e.g., Conner and White 1999; Greene et al. 2010; Schindler et al. 2010) and different life histories can result in dissimilar reproductive success (RS). Lifetime RS of individuals influences trends in population size which affect levels of inbreeding and genetic drift and ultimately the capacity of the population to adapt (Allendorf et al. 2013). Therefore, understanding lifetime RS and the contribution of different life histories within populations is a prerequisite for developing effective conservation strategies and assessing whether current management programs are successful.

The balance between survival and achieving reproduction amid intense male competition in Pacific salmon (Fleming & Reynolds 2004) has contributed to the presence of distinct life history types representing variation in age and size at maturity. Males exhibit multiple life history tactics related to these traits. In Sockeye Salmon *Oncorhynchus nerka*, Chinook Salmon *Oncorhynchus tshawytscha*, and Coho Salmon *Oncorhynchus kisutch*, there are alternate male life history forms: full-size males and precocial males. Full-size males typically maintain access to females by fighting and guarding. Precocial males on the other hand mature earlier and smaller than full-size males and achieve spawning success by taking up satellite positions around the female then sneaking in to release their sperm as the eggs are being laid (Gross 1985).

The current understanding is that precocial male maturation is related to a threshold influenced by both environmental and genetic factors, but these factors are difficult to parse out. Males that mature precociously usually reach the critical maturation threshold of size, growth rate, and energy stored sooner than full size males (Aubin-Horth and Dodson 2004; Piché et al. 2008). Evidence for the genetic component of precocial male maturation in Pacific salmon comes from studies that show: 1) families sired by precocial males have higher rates of precocial males (Iwamoto et al. 1984; Heath 1994); 2) moderate to high heritability (0.49–0.54) of age at maturity (Hankin et al. 1993; see also Heath 1994); and 3) genomic regions and haplotypes associated with age at maturity (McKinney et al. 2021). Precocious maturation has also been linked with size obtained in freshwater (Vøllestad et al. 2004) and hatchery release date (Bilton

et al. 1982), indicating that environmental factors can influence the rate of precocial male maturation, particularly in high-growth environments such as hatcheries (Larsen et al. 2006, 2019). Frequency-dependent disruptive selection is hypothesized to maintain the precocial male life history tactic in the wild (Gross 1985; Fleming & Gross 1994). Precocial males are thought to be more successful at sneaking when they are rare because there are still sneaking positions available and full-size males are focused primarily on battling with other full-size males (Gross 1985).

Numerous observational and experimental genetic studies document the RS of precocial males (referred to as "jacks" in Pacific salmon). The proportion of eggs fertilized by precocial males ranges widely, but can be substantial. One study of Sockeye Salmon found that the percentage of eggs fertilized by jacks ranged from 3 to 93% (Foote et al. 1997). A study of Chinook Salmon found that jacks sired 20% of total offspring at the fry stage (Berejikian et al. 2010). In cases when adult-to-adult RS estimates are not available it is possible to use adult-to-juvenile estimates (Berntson et al. 2011), although the impact of all factors after the juvenile stage are not included. Therefore, adult-to-adult RS estimates are highly valuable, as they provide a more direct measure of Darwinian fitness.

The adult-to-adult RS of precocial males has not been well researched, and their RS relative to full-size males is not well characterized. Studies that have analyzed the RS of hatchery jacks and full-size males separately (Williamson et al. 2010; Thériault et al. 2011; Hess et al. 2012; Janowitz-Koch et al. 2019) have found that jacks typically have lower RS than full-size hatchery-origin males (Koch & Narum 2021). The information on jack adult-to-adult RS and RRS of jacks compared to full-size males outside of a hatchery context is even more limited. It is important to understand how individuals with alternative reproductive strategies contribute to population viability and under what conditions. This is relevant for managing wild populations because the contribution of jacks is often assumed to be negligible and their abundance is not always monitored. Insight on natural age at maturity and mating structure also has implications for hatcheries, as it would inform how breeding methods differ from wild mating systems. In hatcheries that attempt to mate pairs randomly but exclude precocial males, mating is selective. The impact of this divergence from natural mating structure is unknown.

We sought to improve understanding of natural mating structure and jack life history tactic by quantifying jack RS and RRS in a naturally spawning population of Coho Salmon in Auke Creek, Juneau, AK. The access to every individual returning to Auke Creek provided a unique opportunity to study an important life history tactic that has implications for conservation and management. We defined individual RS as the number of offspring that survive to adulthood, which encompasses that individual's mating success, fecundity, and the probability of the offspring's survival. Here we show that Coho Salmon jack males can contribute a substantial amount of returning adult offspring to the population, even though their average RS may be lower than full-size males.

1.3. Methods

1.3.1. Study Population

The study was conducted in the Auke Lake drainage, Juneau, Alaska (Figure 1.1), which supports populations of Sockeye Salmon, Pink Salmon *Oncorhynchus gorbuscha*, and Coho Salmon, as well as Cutthroat Trout *Oncorhynchus clarkii*, Dolly Varden *Salvelinus malma*, Coastrange Sculpin *Cottus aleuticus*, and very few Rainbow Trout *Oncorhynchus mykiss*. The National Oceanic and Atmospheric Administration (NOAA) operates a weir capable of capturing both emigrant and immigrant salmonids independently in the lake outlet, Auke Creek. The weir traps adult salmon on their way to spawn, and each fish is transported over the weir manually, allowing every returning fish to be sampled. The weir also traps emigrating juvenile salmonids. The abundance of Coho Salmon smolts and returning adults (Figure 1.2) has been recorded every year since 1980. Since 2009, all returning adult Coho Salmon have been sampled for genetic analysis: an axillary process is removed and stored in 95% ethanol for later genotyping. Of the returning adult fish, roughly 33% are sampled for age, sex, and length. Age is determined using scales from the preferred area by NOAA personnel following the methods outlined by Hagen et al. (2001). Fish are identified as female, male, or jack based on external morphological characteristics. Jacks are easily distinguishable from full-size males due to no overlap in size distribution (S. Vulstek, NOAA, pers. comm), and females are distinguished from full-size males based on head shape, vent size and shape, and overall body shape. Because all juvenile Coho

Salmon emigrating from Auke Lake are coded wire tagged and adipose clipped, any returning adult possessing an intact adipose fin was identified as a putative stray (i.e., immigrant).

This project used demographic data and tissues from all adult Coho Salmon that returned to the weir from 2009 to 2019. We focused on brood years 2010, 2012, 2013, and 2014, which were the years with the highest ratio of jacks, lowest ratio of jacks, median ratio of jacks, and highest number of spawners, respectively. Auke Creek Coho Salmon spend 1–2 years in freshwater and 0.5–1 year at sea, meaning that they return to spawn between 2 and 4 years after the egg stage (Figure 1.3). Jacks only spend 6 months at sea before returning to spawn, while adult females and full-size males spend a full year at sea.

1.3.2. Genotyping

All returning adult Coho Salmon from 2009 to 2019 were genotyped. Tissue samples were sent to GTseek (<https://gtseek.com/>) for chelex DNA extraction, library preparation, and amplicon sequencing using the ‘genotyping-in-thousands by sequencing’ (GT-seq) protocol (Campbell et al. 2015). The samples were genotyped at a panel of 259 single-nucleotide polymorphism (SNP) loci developed by the Columbia River Inter-Tribal Fisheries Commission for Coho Salmon parentage (Hess et al. no date). After removing loci fixed in Auke Creek Coho Salmon, 251 loci remained for analysis (Appendix 1.1).

1.3.3. Parentage Assignment

We used the program FRANz (Riester et al. 2009) to assign offspring to parents by comparing the genotypes of returning adults to potential parents. This type of parentage analysis is likelihood based, meaning that the likelihood of three individuals being related in a parent offspring triad is compared to the likelihood that they are unrelated. The laws of Mendelian inheritance and other information (e.g., age, sex) are used to narrow down the possible parent combinations. Once the parentage likelihood is calculated, FRANz determines the maximum likelihood pedigree. Statistical confidence in the pedigree is assessed using Markov Chain Monte Carlo (MCMC) sampling.

FRANz runs were conducted for individual return years (2013–2019), allowing us to constrain the candidate set of parents to just the relevant brood years (i.e., 2–4 years prior; Figure 1.3). N_{\max} was calculated for each FRANz run by dividing the total number of potential parents by two and multiplying by 1.10 (to incorporate a 10% buffer in case some of the parents were not genotyped). The genotyping error rate used was 0.01 (the default error rate from FRANz). The maximum number of mismatching alleles allowed between dyads and triples were 5 and 7, respectively. We chose to only include individuals with 60% or more of their loci typed (150 out of 251 loci). Because of uncertainty in field-identified sex, we did not use parent sex in parentage assignment. Parent assignments were accepted if the posterior probability for parent-offspring was ≥ 0.9 .

We did not have known parent-offspring pairs with which to assess parentage assignment error rates. These are errors in which an individual is either falsely identified to a parent, and or not assigned to its true parent. We anticipated a small error rate for this study because a very high (almost all) proportion of returning individuals each year were sampled. Sampling a large proportion of the population decreases the probability that an individual would be paired with the wrong parent. Additionally, the SNP panel had high power (> 100 loci with minor allele frequencies > 0.25 ; Anderson and Garza 2006).

1.3.4. Reproductive Success

We defined individual RS as the number of returning adult offspring assigned to an individual. We examined individual RS results calculated in two different ways: first by using all individuals in the parental dataset and second by using only individuals that produced at least one offspring. Both estimates provide valuable insight on the demographic processes of this population. Averaging the individual RS from the first method represents the actual dynamics of the population, while averaging the individual RS from the second provides information on the range in the number of offspring of successful individuals without being skewed by the abundance of individuals that produced zero offspring (73% of returning individuals from 2009 to 2015 produced zero returning offspring from 2012 to 2019).

1.3.5. Relative Reproductive Success

We defined individual RS (for males) as the number of returning offspring assigned to a focal father and RRS (for each brood year separately) as the ratio of the mean individual RS of jacks to the mean RS of full-size males:

$$RRS = \frac{R\hat{S}_J}{R\hat{S}_F} = \frac{(\sum_{i=1}^{N_J} A_J)/N_J}{(\sum_{i=1}^{N_F} A_F)/N_F}$$

where A_J and A_F are the number of offspring assigned to jack and full-size males, respectively, and N_J and N_F are the total numbers of returning jacks and full-size males for a specific brood year. We determined 95% CIs for RRS estimates following Kalinowski and Taper (2005).

We also calculated the RRS between 3-year-old jacks and 3-year-old full-size males and between 3-year-old full-size males and 4-year-old full-size males. Age refers to the total age of individuals. Comparing 3-year-old jacks and 3-year-old males allowed us to compare fish from the same brood year and maturation age but different life-histories and comparing the RRS of 3- and 4-year-old full-size males allowed us to isolate the impact of age within a single male type.

Two sources of bias in estimates of RS and RRS result from failure to assign offspring to true parents (type A error) or assigning offspring to a false parent (type B error). Both are errors in assignment, which can stem from genotyping error. As stated previously, we did not have empirical data for type A or B parentage assignment error rates. We estimated a range of bias in RRS for a range of type B error rates. The equation used was modified from Araki and Blouin's (2005) correction for bias in RS between hatchery and wild fish in order to account for the very low proportion of unsampled parents in our study. The unbiased relative fitness of jacks (RF_{UNB}) was calculated using the following equation:

$$RF_{UNB} \approx \frac{\hat{F}_J}{\hat{F}_F} \left(1 + \frac{\eta}{\hat{F}_F}\right) - \frac{\eta}{\hat{F}_F}$$

where $\frac{\eta}{\bar{F}_F} \ll 1$, F_J , and F_F are the RS of jacks and full-size males, respectively (A.J. Gharrett, unpubl.).

1.3.6. Immigration into Auke Creek

We examined the abundance and RS of unmarked individuals by return year and sex. Using the parentage data, we determined whether unmarked fish were strays (i.e., individuals that assigned with high confidence to no Auke Creek parents) or were unmarked locals (i.e., individuals that assigned with high confidence to at least one parent from Auke Creek).

1.4. Results

1.4.1. Genotyping and Parentage Assignment

Of the 7,945 individuals sampled, 7,242 (91%) were genotyped at ≥ 150 out of 251 loci scored ($\sim 60\%$ of loci). The percentage of individuals genotyped at ≥ 150 loci and included in further analysis each year ranged from 82% to 99% (Appendix 1.2).

Rates of parentage assignment were high. After filtering out assignments with posterior probability < 0.9 , 78.4% of fish were assigned to two parents, 15.9% to one parent, and 5.8% to no parent. The annual percentage of individuals with zero parents assigned ranged from 3.9% to 11.4% (2014 and 2018 respectively; Appendix 1.2). Parents of unassigned fish were not likely present in our set of candidate parents because the posterior probabilities of the absence of an assignment were all one.

1.4.2. Reproductive Success

When all potential parents were included, RS varied widely between years and sex. The average number of offspring per individual was highest from 2009 to 2011 then dropped below replacement for both sexes from 2012 to 2015 (Table 1.1). Females produced an average of 1.5 (SD=4.4) adult offspring with a range from 0 to 50 offspring per individual from 2009 to 2015. Males (jacks and full-size) produced an average of 0.9 (SD=2.8) adult offspring with a range

from 0 to 36 offspring per individual from 2009 to 2015. Average annual RS of females was consistently higher than that of jacks and full-size males, except for 2015, when the female average RS was slightly less than the full-size male average.

RS also varied between male life history types. Jacks produced an average of 0.7 (SD=1.9) adult offspring, while full-size males produced an average of 1.1 (SD=3.3) adult offspring. The maximum number of offspring produced by a jack and full-size male was 21 and 36, respectively. Except for 2012, the average number of offspring produced and the variance in offspring produced by jacks was consistently less than that of full-size males (Table 1.1).

When only individuals that contributed offspring were considered, we observed the same trend across time and between male types (Figure 1.4). RS was highest from 2009 to 2011 before decreasing. Jacks had lower mean RS and variance in RS than full-size males, except in 2012 (Table 1.1). Again, annual female RS was higher than jacks and full-size males except for one year (2015). Successful females produced an average of 5.2 (SD=6.9) adult offspring while successful males produced an average of 3.6 (SD=4.6) adult offspring. Of the successful males, jacks produced an average of 3.0 (SD=3.1) adult offspring, while full-size males produced 4.0 (SD=5.2) adult offspring.

The number of mates per female ranged from 1 to 9. Of the females that had at least one mate identified, 49.5% only had one male mate. Of the females that had more than one identified male mate, a full-size male contributed the largest number of offspring of all the male mates in 66.2% of cases. This includes all the combinations: mating with only full-size males, only jacks, or a mixture of both male types. For females that mated with at least one jack and one full-size male, a jack sired the majority of offspring in only 14.8% of the pairs.

1.4.3. Relative Reproductive Success

Annual RRS of jack males versus full-size males was consistently below 1, ranging from 0.23 to 0.96 (2010 and 2012, respectively) (Table 1.1). In 2012, there was a sharp increase in RRS, followed by a sharp decline for the rest of the time series. Using all individuals (including those that produced zero offspring) from all years pooled together, the RRS of jacks was 0.57.

The RRS of jacks was generally larger at smaller jack frequencies except for 2015. The year 2015 had the lowest jack frequency of all the years (0.21) and a relatively low RRS (0.32) (Table 1.1). In general, RRS was higher in years where the number of female spawners available was large (Table 1.1).

The RRS of age 3 jacks to age 3 full-size males was less than one in all three years for which we could identify the age of spawners through parentage analysis (2013–2015) and was variable across time. Across all years the RRS of age 3 jacks to age 3 full-size males was 0.52. The RRS of age 3 full-size males to age 4 full-size males was closer to 1, compared with the RRS of age 3 jacks to age 3 full-size males. The RRS of age 3 full-size males to age 4 full-size males ranged from 0.79 to 1.35 (Table 1.2). The overall value across the three years with all the individuals pooled was 1.01.

In examining a range of type B error rate, we found that if the type B error is less than 0.05 the largest percent difference between RRS_{biased} and RRS_{unbiased} across focal brood years would be 2.9% (mean = 1.4%, SD = 1.2%). In other words, our estimates of RRS are likely not heavily biased.

1.4.4. Immigration into Auke Creek

The annual proportion of individuals returning with intact adipose fins (potential immigrants) ranged from 0.84% (2012) to 9.76% (2015) from 2009 to 2015, and most were females or full-size males (Appendix 1.3). Of these individuals, 63.9% were likely strays (assigned with high confidence to no parents); the remaining 36.1% assigned to at least one parent from Auke Creek. Most likely strays were not successful at producing offspring, but one likely stray (a full-size male) had 12 adult offspring and overall, likely strays produced 4.5% of all offspring (2013–2015) produced by the population (Appendix 1.3).

1.5. Discussion

Knowing the RS of individuals with different life history traits is essential for understanding the viability of the population as a whole. Near-complete adult sampling of Coho

Salmon at Auke Creek allowed us to successfully determine the relative reproductive success of jacks to full-size males and to evaluate the typical contribution of jacks to the next generation in a natural mating population. Although jacks were less successful on a per-individual basis, they contributed substantially to the population by fathering 23% of adults returning 2013–2019. Jacks are an important component of population (and by extension, evolutionary) dynamics, indicating that ignoring jacks in the study, monitoring, and management of Pacific salmon is unwise.

1.5.1. Reproductive Success of Jacks

Our finding of reduced RS in jacks, as measured by returning adult offspring, is consistent with research of spawning behavior and success in salmonids. Male size, distance from the female, sperm precedence, and density of other males have all been shown to impact spawning success. Past studies have established that competition between males of different sizes influences access to spawning females (Gross 1985; Schroder et al. 2012), so it makes sense that jacks, being smaller, would have less access to females. Additionally, Berejikian et al. (2010) found that jacks, which typically entered the nest later, had lower adult-to-fry RS than full-size males. They hypothesized that when multiple males are attempting to mate, time of entering the nest determines sperm precedence and thus fertilization success.

The jack life history strategy may compensate for reduced direct access to females to achieve success in multiple ways. First, jacks have a larger gonad mass to body mass ratio than full-size males and jack male sperm is competitively superior to full-size male sperm (Young et al. 2013 and references therein). Second, jacks may benefit from lower levels of marine mortality as a result of spending less time at sea than full-size males. Early marine life, experienced by both jacks and full-size males, may be responsible for less than 37% of variation in marine survival of Auke Creek Coho Salmon (Briscoe et al. 2005), implying that the remaining time full-size males spend at sea accounts for substantial variation in marine survival. Third, jacks may benefit from smaller size during homeward migration and ascent to spawning habitats. Certain commercial fishing methods are size selective and are more likely to intercept full-size individuals (Hamon et al. 2000; Young et al. 2020). Additionally, smaller size may be

advantageous against predation and/or stranding in shallow water on the spawning grounds (Quinn et al. 2001).

The RRS of jacks to full-size males was less than 1 in every brood year analyzed. In each year except 2012, the jack group was roughly half as successful (or less) as the full-size male group. We were not able to examine the relationship between RRS and jack frequencies in a statistically robust way due to the limited number of brood years available for comparison (seven). Despite this, we have confidence in the RRS values themselves. In every year except 2012, the CI for RRS did not include 1.

Interestingly, a large proportion of jacks and full-size males were the same age. The majority of jacks spent 2 years rearing in freshwater and returned to spawn at age 3. These individuals returned at the same age as the full-size males of their cohort who spent 1 year in freshwater and 1 year in saltwater. There were very few jacks that returned to spawn at age 2. Age 3 jacks had lower RS than age 3 full-size males while age 3 full-size males had comparable RS to age 4 full-size males, indicating that RS was more influenced by male type than age.

1.5.2. Immigration into Auke Creek

This study provided a rare opportunity to address reproductive success of immigrant Coho Salmon. Most fish identified as likely strays were not successful at producing offspring; yet overall, they were responsible for ~4.5% of all offspring produced from 2013 to 2015 even though they averaged <4% of spawning adults during those years. These data are suggestive of minimal selection against immigrant individuals, but it would be helpful to confirm the source populations of the strays (likely a mixture of hatchery and wild populations) and to compare the RS of true stray and Auke Creek individuals once more data become available.

1.5.3. Implications for Management and Conservation

Jacks are often not included in studies of wild populations because their small size makes them difficult to enumerate (e.g., at counting towers and in aerial surveys) and they are often assumed to have a small contribution to the next generation. This study shows that jacks can

have a large contribution to RS of returning adult offspring, and that ignoring jacks can drastically influence what conclusions can be drawn from the RS results. For example, consider a scenario in which jacks contribute a significant number of offspring each year but are left out of the counts of returning spawners. The number of fish returning would be attributed to the full-size adult counts in prior years and this would overestimate individual RS and affect projections of population productivity.

Jacks are also relevant to studies that examine the relative RS of hatchery versus natural-origin salmon. The general trend is that the RS of hatchery-origin fish is lower than that of natural-origin fish (e.g., Araki et al. 2008; Koch & Narum 2021), but it depends on the type of hatchery (integrated or segregated) and factors like the source of broodstock and how long fish are held in the hatchery prior to release (Berejikian et al. 2020). Koch & Narum (2021) suggested that precocial males should be accounted for in RS calculations. They found in some studies, when precocial males were analyzed separately from full-size males (which some studies do not do), there appeared to be a smaller difference in the RS of natural- and hatchery-origin individuals when spawning naturally (this was true for both males and females). Overall, including jacks in studies is advisable, because jacks and full-size males may have different mean RS and variance in RS and may represent a substantial portion of the population. Shaul et al. (2011) found that Coho Salmon jacks made up an average of 44% of the male escapement in Auke Creek and <0.5% in the nearby Berners River, suggesting that the effect of excluding jacks when considering RS and population productivity could vary widely even within a single geographic region.

Our study also informs the question of whether, and at what proportion, to include jacks in hatchery broodstock. In hatcheries that attempt to mimic natural conditions to minimize divergence from wild stocks, efforts should be made to include jack fathers at a rate comparable to that in wild populations. Often hatcheries practice random mating of full-size males and females and exclude jacks from their broodstock. This means that their random mating is not truly random. In this case, the current hatchery mating structure of excluding jacks is not representative of the natural mating structure of Auke Creek Coho Salmon, but $RRS < 1$ in our study suggests that including jacks at a rate proportional to their abundance in returning adults

also does not approximate natural conditions. Including jacks may be less crucial in other populations that have fewer jacks or jacks that are less successful. On the other hand, it could be more important in populations where there is naturally a large jack contribution.

When considering adding jacks to broodstock, it is important to acknowledge a complicating factor, specifically how hatchery rearing can affect the resulting broodstock. The proportions of each age class and their subsequent impact on the following generation in a natural population is most likely different from the impact that those same proportions would have in a hatchery setting. Hatchery rearing conditions such as high feed quality and optimal water temperatures increase juvenile growth rate, which influences the probability of early maturation (e.g., Larsen et al. 2004; Thorpe 2004; Knudsen et al. 2006; Larsen et al. 2006; Hankin 2009; Hardstad et al. 2014). This can result in a higher proportion of precocial males than that of the natural population of the broodstock. This higher than natural proportion of jacks conflicts with the goal of integrated hatcheries, which is to not diverge from natural population structure, and also conflicts with segregated hatcheries, which want to produce large fish for harvest. Because there is a component to jacking that is heritable, actively adding jacks into broodstock may only exacerbate this divergence. A study by Larsen et al. (2019) on Chinook Salmon found that while integrated hatcheries slow the rate of genetic change in the threshold for early male maturation, they produce a large proportion of precocial males. This phenomenon makes it difficult to strike a balance between incorporating jacks without adding to the problem of hatchery reduction of age at maturity and overshooting the proportion of jacks in the natural population. Both topics merit further consideration.

Jacking can be a productive life history tactic and it should not be neglected in studies of population and evolutionary dynamics of Pacific salmon. Conservation programs, including hatcheries, would benefit from continued research on the contributions of jacks in natural populations. Additionally, it would be helpful to know the genetic impacts that excluding jacks has on wild populations, which we address in Chapter 2.

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1.7. Figures

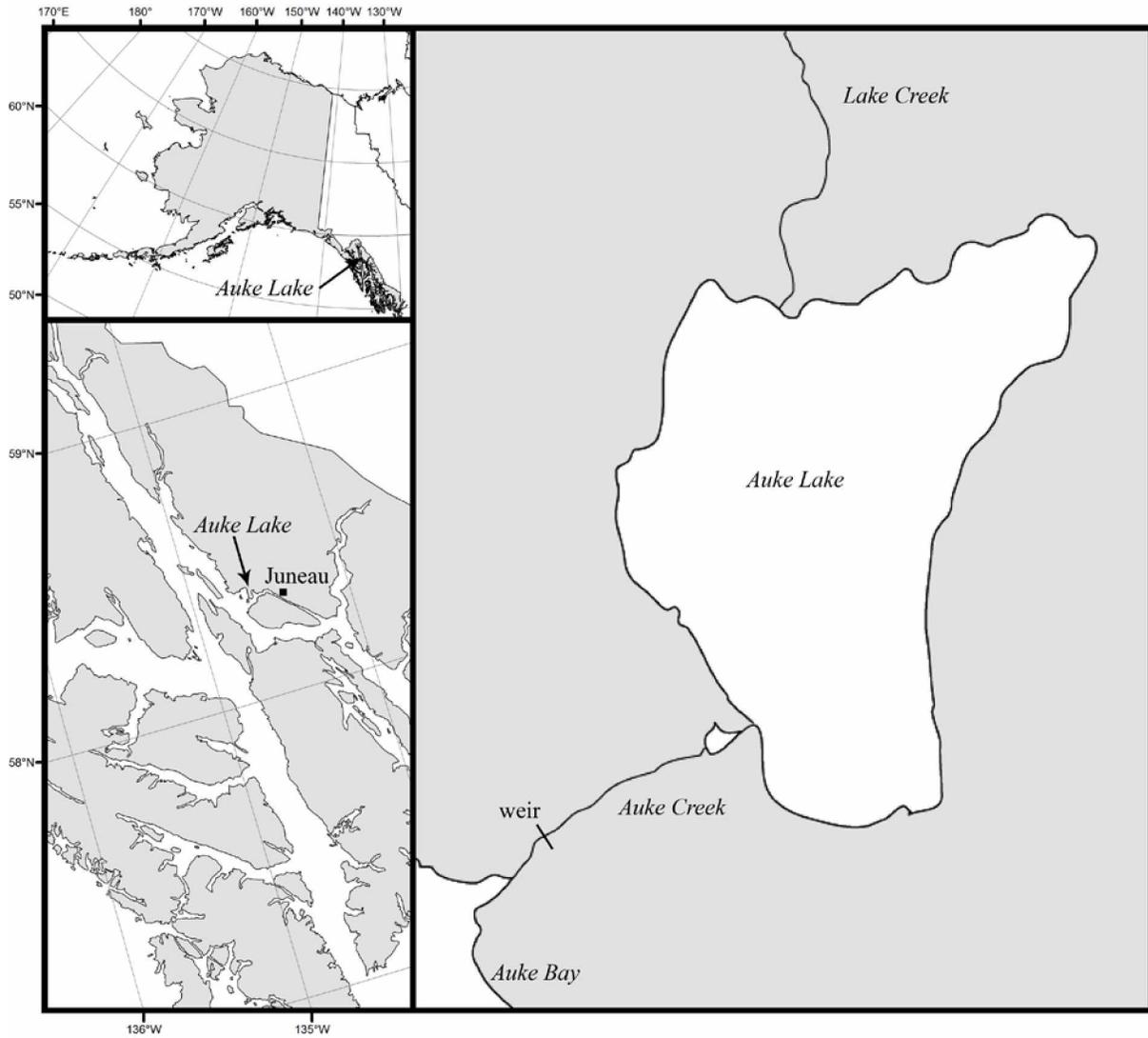


Figure 1.1: Map of Auke Lake system in southeastern Alaska near Juneau. Auke Creek weir is located between Auke Lake and Auke Bay. Map provided by Scott Vulstek.

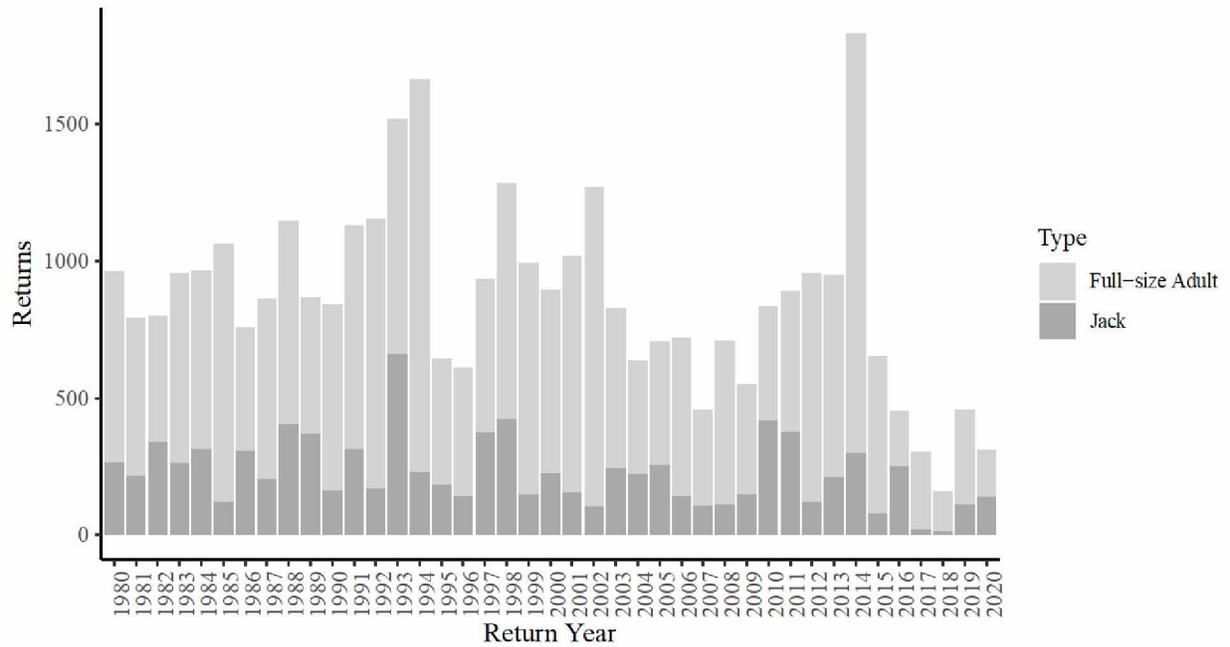


Figure 1.2: Number of returning full-size (male and female) and jack Coho Salmon counted at the Auke Creek weir from 1980 to 2018.

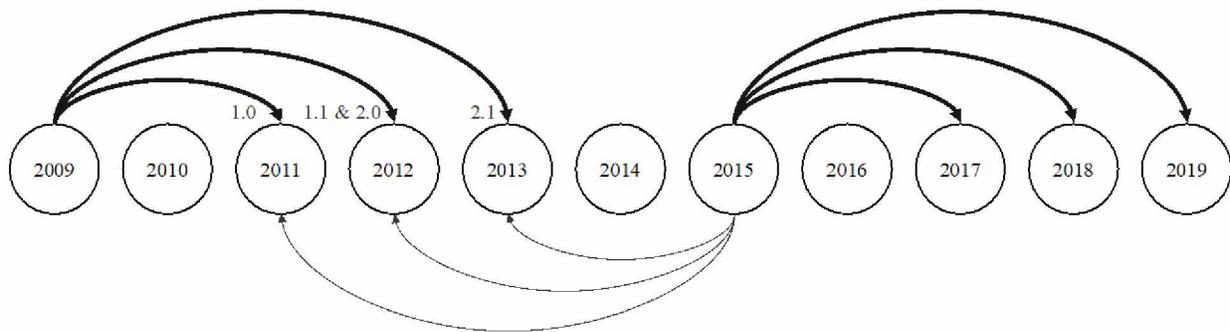


Figure 1.3: Auke Creek Coho Salmon life history diagram. Circles indicate return years (2009–2019). Individuals in this population return 2–4 years after being spawned. Thick black lines relate a single brood (parent) year to all possible offspring return years. Thin grey line relates a single return year to all possible brood years. The number next to each circle indicates the age of the fish. The number before the decimal place is the years spent in freshwater and the number after the decimal point is the years spent in the ocean. For example: 1.0 indicates a fish that spent one year in freshwater and less than a year in the ocean.

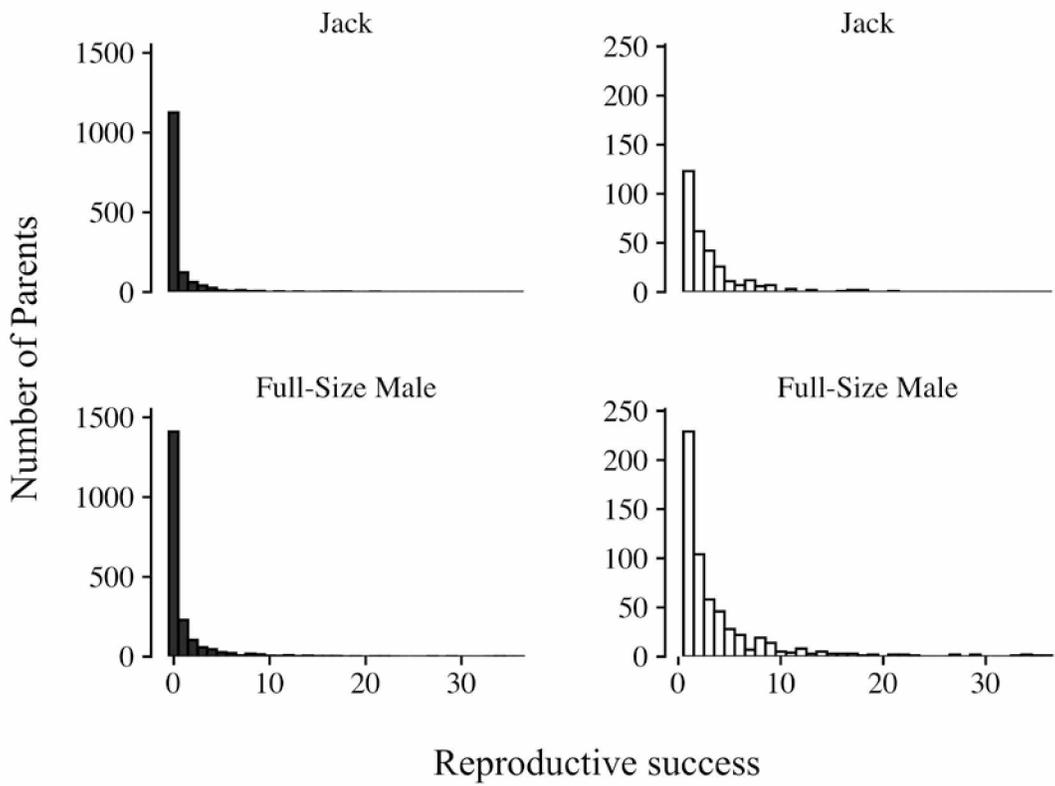


Figure 1.4: Number of Auke Creek Coho Salmon jack males and full-size males and their offspring from 2009 to 2015. The two figures on the left (bars with black fill) include individuals that did not produce offspring while the two figures on the right (bars with white fill) do not.

1.8. Tables

Table 1.1: Auke Creek Coho Salmon demographic and reproductive success reported as mean (SD) for all returning individuals and only returning individuals that produced at least one offspring from 2009 to 2015. Total return abundance (including unknown sex individuals and individuals that were not successfully genotyped). Jack to full-size male relative reproductive success shown with 95% CI.

Year	Total N	Sex ratio (M/F)	Jack frequency	RRS (Jacks:Full-size)	RRS CI	RS of all individuals			RS of individuals with 1 or more offspring		
						Female	Male		Female	Male	
							Jack	Full-size		Jack	Full-size
2009	477	1.55	0.46	0.34	0.27-0.43	2.8 (4.1)	0.8 (1.7)	2.3 (3.3)	5.7 (4.2)	2.8 (2.2)	4.7 (3.3)
2010	816	3.16	0.74	0.23	0.2-0.26	6.9 (9.2)	1 (2.5)	4.6 (6.7)	10.9 (9.5)	3.8 (3.6)	8.1 (7.2)
2011	882	2.10	0.64	0.25	0.22-0.29	3.9 (8.3)	0.9 (2.4)	3.5 (6.8)	11.4 (10.7)	3.6 (3.7)	8.2 (8.5)
2012	958	1.05	0.25	0.96	0.63-1.43	0.5 (1.3)	0.4 (1.4)	0.4 (0.9)	2.4 (2)	2.3 (2.8)	1.8 (1.2)
2013	949	1.34	0.39	0.53	0.39-0.7	0.8 (1.6)	0.3 (0.9)	0.6 (1.4)	2.5 (1.9)	2.1 (1.2)	2.2 (1.7)
2014	1832	1.41	0.28	0.51	0.37-0.68	0.4 (1)	0.2 (0.5)	0.3 (0.8)	1.9 (1.3)	1.4 (0.6)	1.7 (1.1)
2015	656	1.24	0.21	0.32	0.19-0.51	0.6 (1.6)	0.2 (0.6)	0.7 (1.8)	2.8 (2.3)	1.5 (0.8)	2.8 (2.6)

Table 1.2: Auke Creek Coho Salmon male abundance (N), proportion of total return, total offspring produced, mean reproductive success, and variance in reproductive success for each age class from 2013 to 2015. Jacks are age classes 1.0 and 2.0.

Year	Age class	Age	N	Prop.	Total offspring	Mean	Var.
2013	1.0	2	10	0.03	2	0.20	0.40
	1.1	3	54	0.14	28	0.52	0.78
	2.0	3	124	0.32	56	0.45	1.08
	2.1	4	204	0.52	134	0.66	2.19
2014	1.0	2	3	0.00	0	0.00	0.00
	1.1	3	196	0.21	84	0.43	0.86
	2.0	3	263	0.29	46	0.17	0.27
	2.1	4	458	0.50	145	0.32	0.62
2015	1.0	2	13	0.04	3	0.23	0.36
	1.1	3	47	0.15	37	0.79	3.30
	2.0	3	56	0.17	14	0.25	0.45
	2.1	4	204	0.64	151	0.74	3.00

Appendices

Appendix 1.A: Single nucleotide polymorphism panel loci and major allele frequency used for Auke Creek Coho Salmon. Developed for Coho Salmon parentage by the Columbia River Inter-Tribal Fisheries Commission.

Locus	Major Allele Freq.	Locus	Major Allele Freq.
Oki30_5473492	0.4469	Oki_117043_374	0.7028
Oki30_5551409	0.6169	Oki_117144_64	0.7155
Oki_100771_83	0.9153	Oki_117742_259	0.7949
Oki_100974_293	0.8666	Oki_117815_369	0.833
Oki_101419_103	0.5554	Oki_118152_314	0.6811
Oki_101770_525	0.7014	Oki_118654_330	0.5175
Oki_102195_92	0.9056	Oki_120024_226	0.5494
Oki_102213_604	0.6551	Oki_121006_412	0.7681
Oki_102267_166	0.6617	Oki_122138_111	0.6646
Oki_102457_67	0.9028	Oki_122593_430	0.8488
Oki_102801_511	0.8358	Oki_123044_68	0.5216
Oki_103271_161	0.8027	Oki_123921_90	0.7846
Oki_103577_70	0.605	Oki_124162_62	0.5354
Oki_103713_182	0.669	Oki_125998_340	0.79
Oki_104515_99	0.537	Oki_126160_142	0.747
Oki_104519_45	0.6023	Oki_126619_265	0.4734
Oki_105105_245	0.4831	Oki_127645_235	0.8641
Oki_105115_49	0.6937	Oki_128302_547	0.8423
Oki_105132_169	0.6803	Oki_128693_70	0.8349
Oki_105407_161	0.6658	Oki_128757_232	0.9088
Oki_106172_60	0.5911	Oki_128851_185	0.4616
Oki_106313_353	0.7712	Oki_129870_552	0.6981
Oki_106419_292	0.871	Oki_130113_304	0.5683
Oki_106479_278	0.7456	Oki_130295_48	0.8766
Oki_106747_503	0.9086	Oki_130524_184	0.5824
Oki_107031_314	0.4822	Oki_131147_353	0.6448
Oki_107607_213	0.8837	Oki_131460_243	0.5212
Oki_107974_46	0.5812	Oki_131906_261	0.8936
Oki_109525_359	0.5757	Oki_94903_192	0.6802
Oki_109651_152	0.5829	Oki_95318_100	0.53
Oki_109894_418	0.5962	Oki_96158_278	0.6887
Oki_110078_191	0.7391	Oki_96376_63	0.6374
Oki_110381_77	0.7864	Oki_97660_149	0.9381
Oki_111312_141	0.8704	Oki_99550_284	0.6661
Oki_111681_407	0.9414	Oki_RAD100310_36	0.7121
Oki_113457_324	0.4895	Oki_RAD100331_48	0.495
Oki_113979_170	0.8235	Oki_RAD100388_66	0.5818
Oki_114250_187	0.5739	Oki_RAD100479_50	0.6623
Oki_114448_101	0.6637	Oki_RAD100507_58	0.6395
Oki_114587_309	0.6617	Oki_RAD101032_66	0.6385
Oki_116362_411	0.6882	Oki_RAD101136_60	0.5196

Appendix 1.A continued...

Locus	Major Allele Freq.	Locus	Major Allele Freq.
Oki_RAD101478_57	0.6023	Oki_RAD46744_47	0.4618
Oki_RAD101607_45	0.5531	Oki_RAD46974_68	0.6854
Oki_RAD104180_61	0.4658	Oki_RAD47313_50	0.5758
Oki_RAD104335_44	0.8112	Oki_RAD49111_64	0.7527
Oki_RAD104946_41	0.7627	Oki_RAD49348_51	0.6319
Oki_RAD106191_62	0.8937	Oki_RAD51428_47	0.5047
Oki_RAD106666_44	0.5491	Oki_RAD51585_47	0.6932
Oki_RAD109528_55	0.4099	Oki_RAD52040_63	0.8932
Oki_RAD111744_32	0.774	Oki_RAD52785_52	0.5069
Oki_RAD115799_65	0.4634	Oki_RAD53121_66	0.5984
Oki_RAD11844_57	0.8184	Oki_RAD53655_42	0.5518
Oki_RAD12124_45	0.3568	Oki_RAD53703_50	0.5567
Oki_RAD16167_62	0.5769	Oki_RAD53750_45	0.5154
Oki_RAD17541_50	0.4903	Oki_RAD54417_49	0.471
Oki_RAD23788_32	0.8209	Oki_RAD54918_40	0.5062
Oki_RAD25212_35	0.6393	Oki_RAD55090_49	0.4957
Oki_RAD27801_45	0.6272	Oki_RAD55690_46	0.5853
Oki_RAD29028_42	0.6432	Oki_RAD56094_43	0.493
Oki_RAD29136_50	0.7245	Oki_RAD57307_33	0.5596
Oki_RAD34432_38	0.6741	Oki_RAD57826_44	0.7394
Oki_RAD345_59	0.6631	Oki_RAD57956_47	0.6278
Oki_RAD35219_62	0.7888	Oki_RAD58310_55	0.4832
Oki_RAD35990_63	0.8483	Oki_RAD59054_54	0.6267
Oki_RAD36669_48	0.5297	Oki_RAD59556_32	0.5923
Oki_RAD37278_54	0.791	Oki_RAD59920_68	0.5026
Oki_RAD37493_51	0.6457	Oki_RAD59945_45	0.4533
Oki_RAD37537_45	0.6297	Oki_RAD60246_68	0.6453
Oki_RAD37698_60	0.4474	Oki_RAD61746_62	0.8172
Oki_RAD37979_59	0.5146	Oki_RAD61821_61	0.4853
Oki_RAD38077_34	0.2612	Oki_RAD64084_65	0.4892
Oki_RAD40179_68	0.5048	Oki_RAD64627_67	0.7263
Oki_RAD41030_31	0.701	Oki_RAD65234_35	0.4179
Oki_RAD41603_39	0.4776	Oki_RAD65388_37	0.521
Oki_RAD42204_39	0.4873	Oki_RAD65610_58	0.5775
Oki_RAD43051_33	0.2617	Oki_RAD65902_30	0.6675
Oki_RAD43627_30	0.4447	Oki_RAD66265_54	0.6139
Oki_RAD44268_51	0.5596	Oki_RAD66663_68	0.5822
Oki_RAD44444_52	0.727	Oki_RAD66994_58	0.6599
Oki_RAD45691_45	0.5405	Oki_RAD67081_48	0.575
Oki_RAD45878_53	0.6068	Oki_RAD67114_64	0.7302
Oki_RAD46160_48	0.487	Oki_RAD67674_60	0.4386

Appendix 1.A continued...

Locus	Major Allele Freq.	Locus	Major Allele Freq.
Oki_RAD68033_63	0.5052	Oki_RAD87141_55	0.7341
Oki_RAD68190_55	0.5471	Oki_RAD87446_62	0.5033
Oki_RAD69161_64	0.4851	Oki_RAD87621_67	0.7501
Oki_RAD69355_42	0.5569	Oki_RAD87777_48	0.5801
Oki_RAD70262_64	0.5168	Oki_RAD88551_51	0.7133
Oki_RAD70338_46	0.5381	Oki_RAD89259_51	0.7861
Oki_RAD70600_60	0.5918	Oki_RAD89374_40	0.4889
Oki_RAD70812_52	0.5887	Oki_RAD91362_68	0.5681
Oki_RAD70820_47	0.6908	Oki_RAD91430_44	0.6335
Oki_RAD70963_47	0.686	Oki_RAD91470_66	0.6646
Oki_RAD71346_63	0.6357	Oki_RAD91478_52	0.8359
Oki_RAD71442_69	0.5338	Oki_RAD91907_38	0.7158
Oki_RAD71948_56	0.6716	Oki_RAD92875_31	0.8596
Oki_RAD72095_45	0.8415	Oki_RAD93028_59	0.8768
Oki_RAD72101_67	0.7289	Oki_RAD94215_66	0.7258
Oki_RAD72759_48	0.7099	Oki_RAD94241_30	0.5859
Oki_RAD72979_40	0.4827	Oki_RAD96072_42	0.7873
Oki_RAD73094_68	0.5443	Oki_RAD96498_69	0.5726
Oki_RAD73130_59	0.8752	Oki_RAD97325_35	0.6825
Oki_RAD73234_42	0.7046	Oki_RAD97993_40	0.5724
Oki_RAD75909_38	0.4669	Oki_RAD98280_45	0.8807
Oki_RAD75911_69	0.5663	Oki_RAD98485_66	0.5457
Oki_RAD76218_42	0.5936	Oki_RAD99931_47	0.6045
Oki_RAD77207_61	0.6444	Oki_SECC22_67	0.4479
Oki_RAD77210_64	0.5226	Oki_atp4_10	0.5812
Oki_RAD77803_60	0.6963	Oki_arp_105	0.4911
Oki_RAD77883_62	0.5138	Oki_aspAT_273	0.8155
Oki_RAD78112_64	0.5196	Oki_bcaKal_274	0.7697
Oki_RAD78543_33	0.8478	Oki_ca050_17	0.8192
Oki_RAD79761_66	0.5775	Oki_gdh_189	0.7355
Oki_RAD80460_54	0.6625	Oki_gh_183	0.6389
Oki_RAD80645_70	0.6521	Oki_gsh_152	0.8522
Oki_RAD80982_68	0.4814	Oki_hsc713_56	0.8335
Oki_RAD81387_37	0.5179	Oki_hsc71p_313	0.8429
Oki_RAD82856_48	0.5327	Oki_hsflb_85	0.9227
Oki_RAD83766_63	0.5212	Oki_ipa_85	0.8875
Oki_RAD83875_36	0.8183	Oki_nips_159	0.6692
Oki_RAD84577_58	0.4724	Oki_parp3_19	0.11
Oki_RAD85448_48	0.1918	Oki_pigh_33	0.7542
Oki_RAD85949_47	0.5071	Oki_p0p5_265	0.8093
Oki_RAD86627_60	0.824	Oki_sast_230	0.6267

Appendix 1.A continued...

<u>Locus</u>	<u>Major Allele Freq.</u>
Oki_srp09_107	0.8688
Oki_sys1_141	0.5852
Oki_taf12_40	0.0765
Oki_thyK_100	0.8292
Oki_nip_35	0.9158

Appendix 1.B: Genotyping and parentage assignment

Table S.1.B: Number of returning Auke Creek Coho Salmon (female, male, and unknown sex) successfully genotyped from 2009 to 2015 and the percentage of those individuals with zero, one, or two parents assigned from 2013 to 2019. The individuals that were successfully genotyped were used to determine the variance and mean number of offspring produced per individual.

Year	Total N	Genotyped				Not genotyped				Percent Genotyped	Percentage of individuals with 0, 1, or 2 parents identified		
		Female	Jack	Male	Unknown	Female	Jack	Male	Unknown		0	1	2
2009	477	161	117	116	21	17	9	34	2	0.87	-	-	-
2010	816	169	386	138	106	1	10	3	3	0.98	-	-	-
2011	882	254	325	189	6	28	52	26	2	0.88	-	-	-
2012	958	406	72	320	0	61	50	49	0	0.83	-	-	-
2013	949	329	175	273	0	77	36	59	0	0.82	4.5	22.4	73.1
2014	1832	729	284	673	0	31	20	95	0	0.92	3.9	9	87.1
2015	656	288	75	280	0	5	1	7	0	0.98	8.1	18.8	73.1
2016	456	85	244	115	0	3	8	1	0	0.97	7.4	33.3	59.2
2017	303	93	21	92	92	1	0	3	1	0.98	4.4	29.2	66.4
2018	159	55	13	90	0	0	0	1	0	0.99	11.4	5.7	82.9
2019	457	120	109	221	0	1	3	3	0	0.98	8.7	4	87.3

Appendix 1.C: Immigrants into Auke Creek

Table S.1.C.1: Unmarked (adipose fin intact) Coho Salmon returning to Auke Creek (2009–2015). All individuals (marked and unmarked) returning to the weir is ‘All individuals.’ Percent unmarked is the number of marked individuals divided by the number of unmarked and marked individuals. In 2009 and 2010 there were some individuals without a label indicating whether they were marked or unmarked.

Year	All individuals	Unmarked individuals				Total	Percent unmarked
		Female	Jack	Full-size male	Unknown		
9	477	22	0	13	0	35	7.71
10	816	3	5	9	4	21	2.95
11	882	4	1	11	0	16	1.83
12	958	3	1	4	0	8	0.84
13	949	7	3	9	0	19	2.00
14	1832	42	13	54	0	109	5.95
15	656	20	5	39	0	64	9.76

Table S.1.C.2: Percentage and number of Coho Salmon strays (individuals with intact adipose fins and 0 parents) that returned to Auke Creek between 2013 and 2015 and their reproductive success (RS). The percent strays is the number of identified strays divided by the number of successfully genotyped individuals each year.

Year	% strays	Number of strays	Number of strays with 0 offspring	Successful stray RS	
				Min	Max
2013	1.16	9	6	2	4
2014	2.91	49	43	2	3
2015	7.00	45	37	1	12

CHAPTER 2: JACK CONTRIBUTION TO EFFECTIVE POPULATION SIZE IN A NATURALLY SPAWNING SALMON POPULATION²

2.1. Abstract

Little is known about the impact of precocious males on effective population size (N_e) in Pacific salmon *Oncorhynchus spp.*, even though they can make up a large percentage of the total male spawners. We investigated the contribution of precocial males ("jacks") to N_e in a naturally spawning population of Coho Salmon *Oncorhynchus kisutch* from the Auke Creek watershed in Juneau, Alaska. Spawners from 2009 to 2019 (~8,000 individuals) were genotyped at 259 single-nucleotide polymorphism (SNP) loci for parentage analysis. We used demographic and genetic (temporal and linkage disequilibrium) methods to estimate the effective number of breeders per year (N_b). Jack contribution to N_b was assessed by comparing values of N_b calculated with and without jacks and their offspring. Over a range of N_b values (108–406), the average jack contribution to N_b from 2009 to 2015 was 12.9% (SD=9.6%). Jacks consistently made up over 20% of the total male spawners. The presence of jacks did not seem to influence N_b/N . Both the temporal and linkage disequilibrium N_e estimates were biased downwards relative to the demographic estimate, possibly due to immigration. Our results demonstrate that jacks can influence N_b and N_e and can make a substantial contribution to population dynamics and conservation of threatened stocks.

² King, E., M.V. McPhee, S. Vulstek, C.J. Cunningham, and D.A. Tallmon. Jack contribution to effective population size in a naturally spawning salmon population. Manuscript in preparation for Transactions of the American Fisheries Society. Journal subject to change.

2.2. Introduction

Effective population size (N_e) is a useful parameter for conservation because it is inversely related to inbreeding and the loss of genetic variation. In an ideal population, genetic drift is inversely related to the census size of a population, but natural populations often have unequal sex ratio, nonrandom mating, variation in reproductive success, and overlapping generations, which differentiates them from ideal theoretical populations. N_e is the size of an ideal population that experiences the same rate of genetic drift as the actual population being observed (Fisher 1930; Wright 1931, 1938). N_e will either increase or decrease depending on the abundance and reproductive success of individuals of different life history types over a generation. Two important axes of life history variation relevant to N_e are age and size at maturity. In male salmonids, variable age and size at maturity is often associated with alternative reproductive tactics: larger full-size males that compete for females via fighting, and precocial males that mature after spending limited to no time at sea and achieve spawning success using sneaking tactics (Gross 1985).

Within Atlantic Salmon *Salmo salar* populations, the presence of different life history types (in this case precocial males are mature parr) increases N_e (Garcia-Vazquez et al. 2001; Jones and Hutchings, 2001; Saura et al. 2008; Johnstone et al. 2013). In both years of a study, mature parr increased the effective number of males 10-fold and the effective population size two- to three-fold but did not affect the N_e/N ratio (Saura et al. 2008). In a separate study, mature parr increased N_e by balancing the sex ratio and decreasing inbreeding (Garcia-Vazquez et al. 2001). The contributions of mature parr to the maintenance of genetic diversity can span multiple generations. A long-term study of a wild population by Johnstone et al. (2013) found that the addition of mature parr increased the effective population size by up to 4.2 times. Mature parr can increase allelic richness and decrease relatedness of mate pairs because they are from a different age cohort than the females with whom they are mating (Perrier et al. 2014). In populations of conservation concern, the ability of precocial males to increase effective size and allelic richness and to decrease relatedness is valuable for population persistence.

Currently, there is little information on the contribution of precocial males to N_e in natural populations of Pacific salmon. This is surprising given that "jacks" (precocial males that spend limited time at sea) can make up anywhere from <1 to >50% of the male brood year returns (e.g., Sockeye Salmon *Oncorhynchus nerka*, Quinn et al. 2001; Coho Salmon *Oncorhynchus kisutch*, this study). Observational studies of spawning behavior revealed jack participation in spawning (Gross 1985; Healey and Prince 1998) and experimental studies showed jacks can successfully produce offspring. In experimental studies, Sockeye Salmon jacks sired 3–93% of eggs fertilized per female (Foote et al., 1997), and jacks sired 20% of total fry offspring of Chinook Salmon (Berejikian et al., 2010). Van Doornik et al. (2002) indirectly estimated for a population of Coho Salmon that 35% of the effective number of breeders were age-2 jacks. To date, there has been no long-term study to directly calculate the jack contribution to N_e using individual adult-to-adult reproductive success from all individuals in a population, due in part to the difficulty in measuring reproductive success of every individual in a population.

We took advantage of a powerful long-term dataset to determine the contribution of jacks to the effective number of breeders and effective population size over multiple generations in a naturally spawning population of Pacific salmon. We quantified adult-to-adult reproductive success of individuals over 11 years in the Auke Creek population of Coho Salmon. Our specific objectives were to i) quantify the contribution of jacks to N_b and N_e using demographic and genetic methods (temporal and linkage disequilibrium); ii) compare N_b and N_e estimates among methods; and iii) estimate age-specific contributions to N_b and N_e using life tables. We found that, jack life history contributes substantially to N_b and N_e , and we discuss potential implications for small and declining stocks of Pacific salmon.

2.3. Methods

2.3.1. Study Population

This study was conducted on a population of Coho Salmon in the Auke Lake drainage in Juneau, AK. Tissue samples and demographic information were collected from a permanent two-

way weir located between Auke Lake and Auke Bay that is operated by the National Oceanic and Atmospheric Administration (NOAA). Counts of out-migrating smolts and returning adults have been recorded annually since 1980 and genetic samples have been collected since 2009. The weir catches all out-migrating smolts and the smolts are released downstream after their adipose fin is clipped and they receive a coded-wire tag. The weir also captures all returning adults. As each individual is manually transported over the weir, it is tissue sampled (axillary process which is then stored in 95% ethanol) and assigned a sex/type (female, full-size male, or jack male) based on morphological characteristics. Roughly one third of returning adults are sampled for length and age. Adults without intact adipose fins are potentially strays. This study uses data from adults returning between 2009 and 2019. Auke Creek Coho Salmon females typically return 3 or 4 years after being spawned (1–2 years in freshwater and 1 year at sea). Males either return at age-2 (1 year in freshwater and 6 months at sea), 3 (2 years in freshwater and 6 months at sea or 1 year in freshwater and 1 year at sea), or 4 (2 years in freshwater and 1 year at sea). Males that return after 6 months at sea, regardless of freshwater age, are referred to as jacks and are smaller than males that spent a full year at sea.

2.3.2. Genotyping and Parentage Assignment

Genotyping and parentage assignment methods were the same as those presented in Chapter 1. In brief, we employed a contract lab (GTseek) to extract and sequence tissue samples of all returning individuals from 2009 to 2019 using ‘genotyping-in-thousands’ (GT-seq) protocol (Campbell et al. 2015). The single-nucleotide polymorphism (SNP) panel used, composed of 259 loci, was developed specifically for Coho Salmon parentage by the Columbia River Inter-Tribal Fisheries Commission (Hess et al. no date).

We used the program FRANz (Riester et al. 2009) to assign parentage for adult offspring from each individual return year from 2013 to 2019. We constrained the set of possible parents for each year to fish that returned 2–4 years prior. Sex was not used in parentage assignment. For each FRANz run we used the following parameters: N_{\max} was calculated by multiplying the number of potential parents, as enumerated at the weir, by $(1.1)/2$ (half of the potential parents with a 10% buffer); genotyping error rate was assumed to be 0.01 (default FRANz value); the

allowed maximum number of mismatching alleles was 5 for dyads and 7 for triads; and the minimum loci typed per individual was 150 (out of 251). Parentage assignments with posterior probability less than 0.9 were discarded. We expected assignment error to be small because we genotyped such a large proportion of the population. For additional details, see Chapter 1.

2.3.3. Demographic Estimate of N_b and N_e

Parentage assignment allowed direct calculation of the inbreeding effective number of breeders (N_{bD}) in the population each year, and from this demographic information, an inbreeding effective population size (N_{eD}) was calculated for each generation (for full notation see Table 2.1). N_e estimates apply over a generation (4 years for Auke Creek Coho Salmon) while N_b estimates are annual. First, we calculated N_{bD} of each sex for each return year from 2013 to 2019 using population size (N), mean number of offspring (\bar{k}), and variance in the number of offspring per individual (V_k) with the following equation (Crow and Kimura 1970; Caballero 1994):

$$N_{b[i]}^{female} \approx \frac{\bar{k}_f N_f - 2}{\bar{k}_f - 1 + V_{kf}/\bar{k}_f}, \quad N_{b[i]}^{male} \approx \frac{\bar{k}_m N_m - 2}{\bar{k}_m - 1 + V_{km}/\bar{k}_m}$$

After this we calculated the net N_{bD} for each year [i] using the male and female effective number of breeders with the following equation (Wright 1931; Crow and Kimura 1970):

$$N_{b[i]} = \frac{4(N_{b[i]}^{female} \cdot N_{b[i]}^{male})}{(N_{b[i]}^{female} + N_{b[i]}^{male})}$$

Then N_{eD} values for different generations were estimated using N_{bD} estimates from the corresponding years in each generation:

$$N_{eD} = \frac{1}{\sum(X_i^2/N_{b[i]})}$$

where X_i is the proportional contribution of breeders from year i to the next generation (Waples 2002; Araki et al. 2007).

Coho Salmon return to Auke Creek up to four years after being spawned, so for each generation, we used four different N_{bD} values. Over the time series of 11 years, we calculated four N_{eD} values using overlapping N_{bD} values with a sliding scale of four years (2009–2012, 2010–2013, 2011–2014, and 2012–2015). Individuals that were not successfully genotyped were included in the calculations of sex-specific N_b and were assumed to have the same mean and variance in reproductive success as those successfully genotyped of the same sex. In 2010, of the 816 individuals that returned, 109 were not assigned a sex. In each of 400 iterations, we randomly assigned the unsexed fish a sex (given a 50:50 sex ratio) and then calculated N_{bDf} , N_{bDm} , and N_{bD} . To estimate 2010 N_{bD} , we used the mean N_{bD} from all 400 iterations. Estimates of N_{bD} for 2010 and N_e for generations including 2010 using a 50:50 sex ratio were almost identical to using the average sex ratio (58:42) from 2009, 2011, 2012, 2013, 2014, and 2015.

To examine the sizes of N_{bD} and N_{eD} relative to the population size we calculated two ratios. In N_{bD}/N , N represents the number of individuals returning to spawn in a single year, whereas N in N_{eD}/N represents the total number of individuals returning over the entire generation (which includes multiple spawning/return years).

To investigate the specific contribution of jacks to N_{bD} , we also calculated N_{bD} using the same dataset but removing all jack parents and their offspring (after Saura et al. 2008 and Perrier et al. 2014). Jack contribution was defined in the following way:

$$JackContribution = 100 * \frac{N_{bD}withjacks - N_{bD}withoutjacks}{N_{bD}withjacks}$$

Jack contribution represents the percent difference in annual estimates of N_{bD} when jacks are excluded from calculations. Positive values indicate that the presence of jacks increases N_{bD} .

We made three choices when excluding jacks from the dataset. First, we excluded the year 2010, because there was a high proportion of unidentified sex/type (i.e., jack vs. regular

male) samples that year and this analysis relied on comparing totals of full-size males and jacks in the population. Second, we excluded all parents of unidentified sex/type across all years. Third, mean and variance in reproductive success were calculated with the number of retained individuals that were successfully genotyped. We assumed that the individuals not successfully genotyped had the same reproductive success as those that were successfully genotyped. In the calculation of N_{bD} , the total N included all individuals (genotyped and not genotyped). We expect the bias introduced by calculating N_{bD} this way to be small given the high rate of genotyping success (92% of all individuals from 2009 to 2019) we achieved.

2.3.4. Genetic Estimates of N_b and N_e

N_b was estimated using the linkage disequilibrium (LD) method (N_{bLD}) (Hill 1981; Waples 2006; Waples & Do 2008) as implemented in NeEstimator V2.1 (Do et al. 2014) and the temporal method of Waples et al. (2007) in the program SALMONNb (N_{bS}). For N_{bLD} and N_{bS} , we analyzed individual cohorts (individuals born in the same year) for each year 2009 to 2015. Individuals were grouped into cohort years using parentage-based aging. Bias in the estimates of N_{bLD} was corrected using the haploid number of chromosomes (Waples et al. 2016), which for Coho Salmon is 30 (Uyeno 1972).

N_{eT} was calculated using the temporal method (N_{eT}) of Jorde and Ryman (2007) as implemented in NeEstimator V2.1 (Do et al. 2014). The first and second sample of returning adults were 2009 and 2019, respectively, and the lowest allele frequency used was 0.05. Returning adults were sampled non-lethally with replacement before mating (Plan I under the discrete generations model of Waples 2005). Therefore, our estimate of N_{eT} represents the harmonic mean effective population size in generations 0 through $t-1$ (Waples 2005).

We converted annual N_{bD} and N_{bLD} to N_e per generation, which allowed us to compare the results to N_{eT} . Since N_{eT} applies from generations 0 to roughly 2, and 2 generations of 3.72 years was roughly seven years, we calculated the harmonic mean N_b using seven years of data (2009–2015). The generation length of 3.72 years is a representative value for this population

calculated using composite life tables with information from 2013 to 2015. To get N_e , we multiplied the harmonic mean value by the average generation time (g) of 3.72 years.

2.3.5. Using Life Tables to Estimate Effective Population Size

Life tables describe the abundance, survivorship rate, and offspring produced for each age group in a population or species. Life tables can be used to calculate the number of offspring produced from each age group, based on the proportions of individuals at each age and the mean and variance in number of offspring of individuals in each age group. For iteroparous species, individuals can reproduce at multiple ages and each row of the life table represents each year of an individual's life. But in semelparous species, all individuals die after reproducing, and in this case the life table describes individuals that return to spawn in a single year and there is a row for each age individuals return to spawn. For example, Auke Creek Coho Salmon females spawn at ages 3 or 4, so the female life table has a row for age 3 individuals and age 4 individuals.

We created one composite life table for each sex using either all males or females from 2013 to 2015. These years were chosen because they were the only years for the study where we had parentage-based age estimates (needed for separating the population into age classes) and samples of all possible returning offspring from these individuals (needed to calculate reproductive success of the individuals). To create each life table, we first determined the number of individuals in each age class. For males, we used the age classes 1.0, 1.1–2.0, and 2.1, where the number before the decimal denotes the inferred number of years an individual spent rearing in freshwater and the number after the decimal denotes the number of years an individual spent in the ocean before returning to spawn. The corresponding ages of those age classes are 2, 3, and 4 years old respectively. Freshwater age was deduced by subtracting the saltwater age (known based on male type) from the total parentage-based age of an individual. For females we used the age classes 1.1 and 2.1 (age 3 and 4 respectively) because all females spend a full year at sea.

For each age class within the group, we determined the number of individuals, mean number of offspring produced, and variance in number of offspring produced. With this age-

specific information, we calculated the total number of offspring produced, the net variance in reproductive success for the whole table, the effective number of breeders, and the generation length (g). Each sex-specific g was calculated as the sum of each age class multiplied by their relative contribution of offspring. We then combined the male and female table information to determine overall N_{bLT} , g , and N_{eLT} ($N_{eLT} = g * N_{bLT}$).

After creating the composite table, we explored how modifying the composition of N affected the population parameters N_b , N_e , and g . To examine the contribution of jacks to the hypothetical composite population's effective population size, we created an alternate scenario: The total number of males remained the same, but all jacks were replaced by full-size males. The ratio of 1.1 jacks to 2.1 full-size males was kept the same. To analyze this scenario, we created a male composite life table with the age-3 group separated into age-3 jacks (2.0) and age-3 full-size males (1.1). In a typical life table, each age class represents a specific integer age, but in our salmon population the two types of males have different survival, fecundity, and reproductive success due to differing years spent in freshwater and saltwater (Chapter 1). Splitting the age class also allowed us to investigate the impact of manipulations to the life table such as varying the number of jacks. For our new scenario we calculated N_{bLT} , g , and N_{eLT} using the same methods as the original composite table.

2.4. Results

2.4.1. Demographic Estimate for Auke Creek Coho

Effective number of female breeders each year ranged between 50 and 167, while the effective number of male breeders ranged from 59 to 259. In all 6 years analyzed, the effective number of male breeders exceeded the effective number of female breeders. Combined, the total N_{bD} ranged from 108 to 406 (Table 2.2). Over the time series, N_{bD} relative to the census size each year declined rapidly and then increased (Figure 2.2). N_{bD}/N oscillated between 0.30 and 0.15 from 2009 to 2015. Assuming four years per generation, the maximum N_{eD} was 809 and the minimum was 384 (Table 2.3). The range of N_{eD}/N was 0.08–0.18.

Mean annual jack contribution to N_{bD} was 12.9% (SD=9.6%). Jacks generally increased N_{bD} via male-specific values, N_{bDm} , with little impact on female-specific values, N_{bDf} (Table 2.2). Mean annual jack contribution to N_{bDm} was 24.2% (SD=15.2%), and jacks increased N_{bDm} in every year except 2012. Excluding jacks had a smaller impact on N_{bDf} than N_{bDm} ; mean annual jack contribution to N_{bDf} was 0.9 (SD = 5.0). In two of six years, N_{bDf} without jacks was greater than N_{bDf} with jacks because excluding jacks decreased the female variance in reproductive success which increased N_{bDf} . In 2012, N_{bDf} without jacks was larger than N_{bDf} with jacks and N_{bDm} without jacks did not change, so the overall N_{bD} without jacks (174) was larger than N_{bD} with jacks (169) and jack contribution was negative (-3.0%). N_b / N did not notably change when jacks were excluded. For each year, the difference between N_b / N with and without jacks was <0.05 because reducing N also reduced N_b .

2.4.2. Genetic Estimates of N_b and N_e

N_{bLD} (range: 98 to 271) and N_{bS} (range: 74 to 180) followed the same overall pattern of N_{bD} (Figure 2.2): a gradual increase from 2009 to 2014 then a steeper decline to 2015. N_{bD} , N_{bLD} , and N_{bS} estimates apply to the year in which the parents of genotyped individuals reproduced (Waples 2005). We estimated N_{eT} to be 218 (180–260 parametric 95% CI; 186–264 jackknife CI). N_{eD} was 611 and N_{eLD} was 433.

2.4.3. Using Life Tables to Estimate Effective Population Size

The composite life tables for males and females created from our demographic data revealed that the overall g was 3.72 years (Male: 3.61, Female: 3.84), N_{bLT} was 564 (Male: 306, Female: 261), and N_{eLT} was 2098 (Table 2.4). Full-size males contributed the most offspring, but the contribution from jacks was still substantial (jacks produced 17.3% of offspring in the table). Most of the jack contribution was from age-3 jacks, as age-2 jacks were less common (5.5% of jacks were age-2). Overall, jacks had smaller mean and variance in reproductive success than full-size males, but similar mean adjusted variance. Age-4 females had similar reproductive success to age-3 females, but their higher abundance resulted in a greater contribution of offspring than age-3 females.

Having age class information allowed us to make predictions of how the removal or inclusion of jacks impacted N_{eLT} . For the modified scenario, using the same number of adults but only full-size males, the overall g increased to 3.75 years, the overall N_{bLT} increased from 564 to 586, and the total N_{eLT} increased from 2098 to 2,196. Even though removing jacks increased the variance in male reproductive success, N_{bLT} for this case was slightly larger than the original case because of the increase in the male mean number of offspring. N_{eLT} for this case was slightly larger than original because of the larger g and N_{bLT} . The impact of excluding jacks on N_{eLT} in this case was small, resulting in less than a 5% increase in N_{eLT} .

2.5. Discussion

Our study yielded some important insights into the life history variation and effective population size of this population. First, jacks made a substantial contribution to N_e , but their contribution varied widely across years. Jack Coho Salmon in Auke Creek made up a large proportion of the spawning males in some years and contributed a significant number of offspring. Excluding jacks from N_e calculations could result in underestimates of N_e and faulty conclusions about the status of populations being monitored using N_e . Second, demographic, LD estimates, and temporal (SALMONNb) N_b produced similar results and reflected changes in adult census abundance over time, although the temporal N_e estimate spanning 2009–2019 was lower than N_e from the other methods. Third, the life table manipulation for this population indicated that replacing all jacks with full-size males did not result in a substantial increase in N_e (less than 5% increase in N_e between cases), underscoring the jacks contribution to N_e .

2.5.1. Impact of Jacks on N_e

The presence of jacks in this population generally increased N_b (male and overall), but the magnitude of the contribution was highly variable from year to year. Removing jacks decreased the number of males and typically increased the variance in reproductive success which lowered N_{bm} . Reductions in N_{bD} were primarily caused by the smaller numbers of individuals because removing jacks had little effect on N_b / N (the difference between the two estimates was consistently <0.05). Similarly, a study on Atlantic Salmon found that including

mature parr increased N_e without changing N_e/N (Saura et al. 2008). Although there is no consensus on the typical range of N_e/N values for natural populations of plants and animals (Waples 2002), the N_{eD}/N for Auke Creek Coho Salmon (0.08–0.18) is comparable to the values reported for a wide range of species. Frankham (1995) first reported that N_e/N averaged ~ 0.11 over 100 species and a more recent review by Palstra and Ruzzante (2008) found a median N_e/N of 0.14.

We found little effect of removing jacks on N_{bDf} , which aligns with a study on Atlantic Salmon that found that mature parr exclusion or inclusion had a negligible impact on female N_e (Perrier et al. 2014). We did observe one year when N_{bDf} was larger without jacks because removing jacks decreased the variance in female reproductive success. The N_{bDm} that year did not change after removing jacks, so overall N_{bD} without jacks was slightly larger than with jacks. The lack of influence on N_{bDf} suggests that females in this population are not male limited. Females are the less abundant sex and 88% of females with at least one identified mate had one or more full-size male mates.

Jack influence on N_{bD} and N_e is complex and varies with sex ratio and jack frequency. Jacks impact N_b by reducing mean male reproductive success and variance in reproductive success which will impact N_e (the product of N_b and generation length) assuming constant generation length.

2.5.2. Comparison Across Estimates

All N_b estimates seem to show a similar pattern and reflect the dynamics in census size. N_{bD} values were similar to N_{bLD} values. While the N_{bLD} values were slightly lower than the N_{bD} values, they still followed the same trend for the entire series. Other studies have also found close relationships between demographic and LD estimates of N_b , yet comparisons on this scale are still relatively rare. A study of the impact of Atlantic Salmon mature parr on N_b found that the demographic estimate (220) and LD estimate (198) were very similar (Perrier et al. 2014). Serbezov et al. (2012) found similar demographic N_b (40) and LD N_b (53) in a population of Brown Trout *Salmo trutta*.

N_e from the demographic method ($N_{eD} = 611$) was larger than the temporal ($N_{eT} = 218$) and LD (N_{eLD} was 433) methods. The genetic estimates may be lower than the demographic estimate because of immigration and/or how the different methods are affected by fluctuations in population size throughout the time series. The legacy effects of immigration and past small population sizes can carry over among years and depress genetic estimates of N_e . For example, the temporal method was calculated using the genetic data from individuals from 2009 and 2019, and this time period spanned both the increase to an all-time high number of returns and then an all-time low. This fluctuation in dynamics might be why the temporal estimate is lower than the other estimates. The demographic estimate is not as impacted by small population sizes as the genetic estimates because there are no genetic effects involved when calculating N_{eD} from demographic information.

The amount of migration into the population and the reproductive success of strays will likely influence our genetic estimates of effective population size because stray fish, unclipped fish with no assigned parents, contributed 4.5% of offspring produced 2013 to 2015 (Chapter 1). A mean of 5.6% returning fish per year had un-clipped adipose fins (range 0.8%–11.3%). The presence of strays in the Auke Creek population could be why N_{bLD} is slightly lower than our demographic estimate of N_b and why N_{eLD} and N_{eT} were smaller than N_{eD} . Ryman et al. (2019) found that even one migrant per generation can cause differences among the N_e estimates of commonly used methods in a modeled population with discrete generations. They suggested that migration could potentially result in LD $N_e >$ temporal N_e for a local population, but also warned that their on-going work suggests census size may also affect variance N_e . Identifying the source of strays and the size, structure, and migration rates of regional subpopulations of Coho Salmon in Southeast Alaska will improve our understanding of how immigration would affect our various N_b and N_e estimates.

2.5.3. Insights from Life Tables

After manipulating the life table, we concluded that removing jacks and replacing them with full-size males had a small impact on N_{eLT} , increasing it by <5%. This suggests that, even though jacks have a smaller average reproductive success per individual, replacing them with

more successful males has less of an impact than might be expected. This occurred because jack presence reduced variance, and when jacks were removed, variance increased and dampened the increase in N_{bLTm} that occurred from the increase in k . An increase in male variance after jack removal is consistent with what we observed in our N_{bD} calculations.

2.5.4. Conservation Implications

Monitoring the effective population size of Auke Creek Coho Salmon is important because returns declined to an all-time low (since weir operation started in 1980) of 159 individuals in 2018, and it is unclear whether the trend will continue. There was a slight increase in 2019 (457), 2020 (309), and 2021 (365), but these years were still low compared to the long-term average (prior to 2014) return of 924 including jacks and 675 excluding jacks. The escapement goal set for Auke Creek Coho Salmon (jacks excluded) is 200–500 (Clark et al. 1994). From 2009 to 2017, 2019, and 2021, the escapement either met or exceeded this goal, but not in 2018 and 2020. Monitoring the contribution of each life history type in this population and others will provide insight into the population dynamics of declining stocks, which may facilitate conservation efforts for vulnerable populations.

Understanding the contribution of different life history types provides insight into how populations may respond to stressors such as climate change and habitat degradation. Perrier et al. (2014) found that mature Atlantic Salmon parr increased N_b and allelic richness and hypothesized that the presence of mature parr may compensate for low amounts of returning anadromous males and potentially slow the decline in N_e . Jacks, by spending less time at sea, might help compensate for low full-size male returns in periods of high marine mortality. In this population, jacks increased N_b in most years.

An ability of jacks to bolster N_e would depend on the relationship between jack influence on N_b and the proportion of jacks on the spawning grounds. Jacks tend to have lower reproductive success at higher jack frequencies (Berejikian et al. 2010), which may affect their contribution to N_b and N_e . We observed the lowest levels N_b/N (0.14 and 0.16) at high (0.64) and low (0.21) jack frequencies. The highest N_b/N (0.31) occurred at a moderate jack frequency

(0.46). Additional insight on the relationship between jack frequency and the magnitude of influence of jacks on N_b/N would be very valuable for this population of Coho Salmon and many others and requires more years of data. This would inform whether there is buffer capacity for N_b and N_e against declines in full-size male returns, and if so, how much.

Additional areas that warrant future research are gene flow between brood years, immigration into the population, and environmental and habitat constraints. This study demonstrates that gene flow and immigration are occurring, but their full impact is unknown. Potential effects could include decreases in inbreeding and/or outbreeding depression. Additionally, it is likely that the effective population size of Auke Creek Coho is affected by environmental factors such as temperature and stream flow. A study on Brook Trout *Salvelinus fontinalis* highlighted a relationship between stream discharge and N_b and the authors suggested that management actions based on habitat improvement may have more of an impact on N_b than attempts to increase abundance (Whiteley et al. 2015). The link we have demonstrated between an alternative life history type and N_b will be relevant when considering the impact of environmental factors on N_b and will help inform conservation strategies for Pacific salmon.

2.6. References

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2.7. Figures

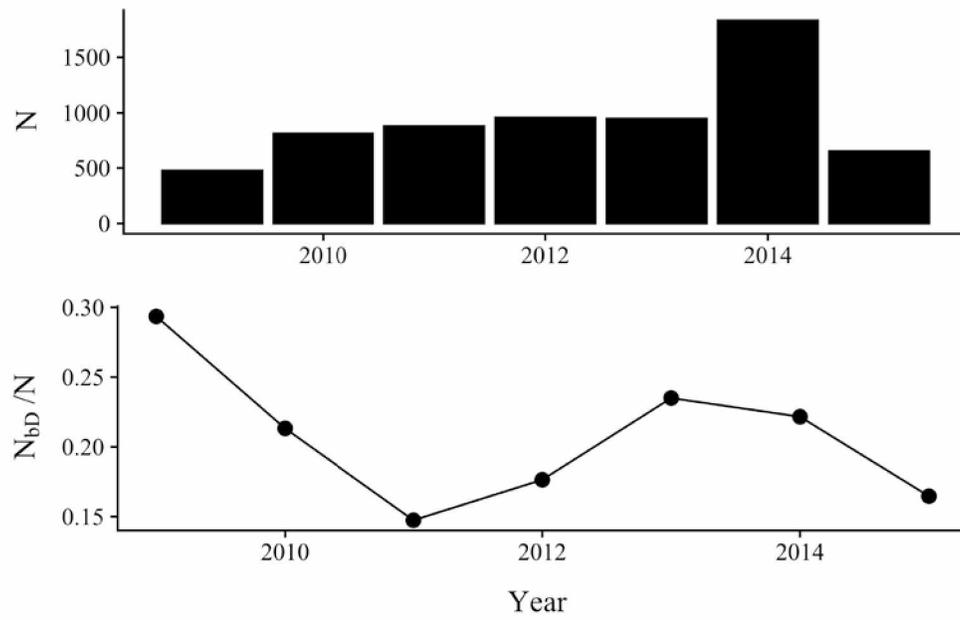


Figure 2.1: Temporal patterns in census size (N ; top panel) and the ratio of effective number of breeders, calculated using demographic information, to census size (N_{bD}/N ; bottom panel) of Auke Creek Coho Salmon, 2009–2015. Census size was calculated using all individuals (including those with unknown sex/type).

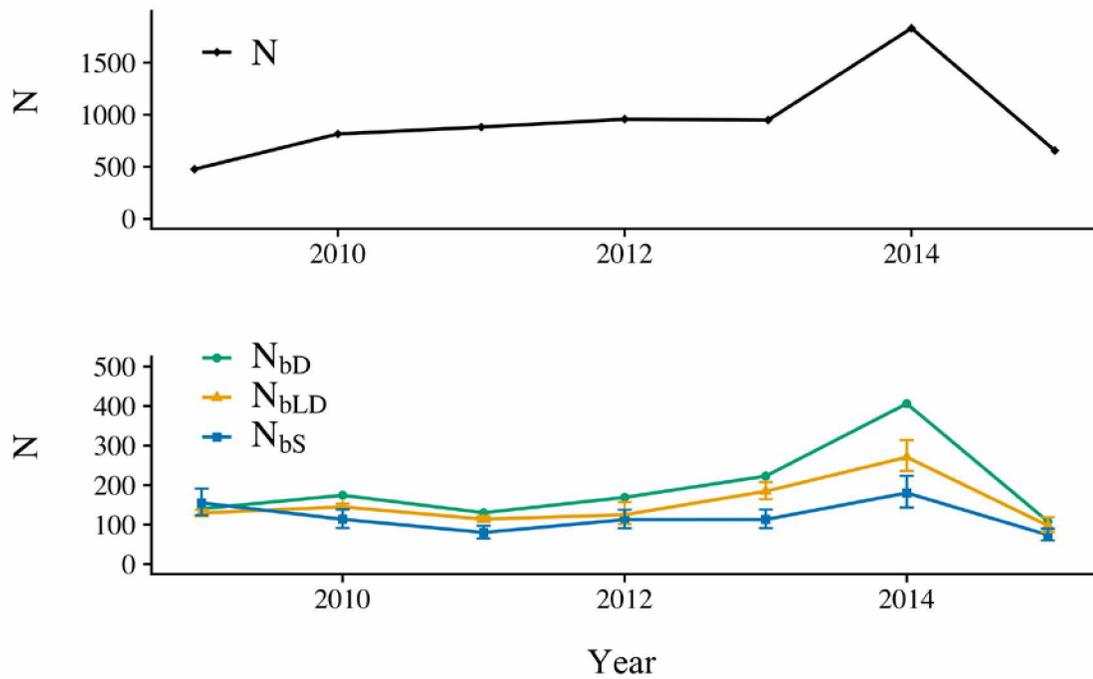


Figure 2.2: Temporal patterns in the total census population size including unknown sex/type individuals (N), inbreeding effective number of breeders over time using the demographic method (N_{bD}), linkage disequilibrium method (N_{bLD}), and SALMONNb method (N_{bs}) for Auke Creek Coho Salmon from 2009 to 2015. 95% CIs are included (for N_{bLD} and N_{bs}) but are too small to see in some cases. Notice the difference in scale for the top panel.

2.8. Tables

Table 2.1: Notation used to describe demographic and genetic parameters in this paper.

Term	Definition
N	Census population size.
N_e	Effective population size. Applies to an entire generation.
N_b	Effective number of breeders. Applies to a single reproductive cycle, which is one year for Pacific salmon.
N_{eD}	Effective population size calculated using demographic information.
N_{bD}	Effective number of breeders calculated using demographic information.
N_{bDf}	Effective number of female breeders calculated using demographic information.
N_{bDm}	Effective number of male breeders calculated using demographic information.
N_{eLD}	Effective population size calculated using the linkage disequilibrium method.
N_{bLD}	Effective number of breeders calculated using the linkage disequilibrium method.
N_{bS}	Effective number of breeders calculated using the SALMONNb method.
N_{eT}	Effective population size calculated using the temporal method.
N_{eLT}	Effective population size calculated using the life table method.
N_{bLT}	Effective number of breeders calculated using the life table method.
\bar{g}	Generation length.
\bar{k}	Mean number of offspring produced per individual.
V_k	Variance in number of offspring produced per individual.

Table 2.2: Demographic information and effective number of breeders (N_b) calculated using the demographic method (N_{bD}) for Auke Creek Coho Salmon. Number of returning individuals in this table excludes individuals with unknown sex and return year. Jack frequency is the ratio of jacks to all males. N_b values under ‘All’ were calculated using all individuals and values under ‘No jacks’ were calculated with all jacks and offspring of jacks removed. Percent jack contribution is the percent difference between N_b with and without jacks included in N_b .

Year	Number returning individuals				Sex ratio (M/F)	Jack frequency	N_b						Percent jack contribution
	Female	Full-size male	Jack male	Total			Female		Male		Total		
							All	No jacks	All	No jacks	All	No jacks	
2009	178	150	126	454	1.55	0.46	64	62	78	54	140	115	17.9
2011	282	215	377	874	2.10	0.64	54	53	83	46	130	98	24.6
2012	467	369	122	958	1.05	0.25	77	82	94	93	169	174	-3.0
2013	406	332	211	949	1.34	0.39	107	105	116	80	223	182	18.4
2014	760	768	304	1832	1.41	0.28	167	172	259	196	406	367	9.6
2015	293	287	76	656	1.24	0.21	50	46	59	51	108	97	10.2

Table 2.3: Auke Creek Coho Salmon effective population size (N_e) calculated using yearly effective number of breeders (N_b) values and the proportional contribution of offspring from each year. Mean yearly N is the average number of the individuals returning each year in the generation and Total N is all returning individuals in the generation. These census values do not include individuals with unknown sex/type.

Generation	N_e	Mean yearly N	Total N	N_e/N
2009-2012	468	748	2993	0.16
2010-2013	446	872	3488	0.13
2011-2014	384	1153	4613	0.08
2012-2015	809	1099	4395	0.18

Table 2.4: Female and male composite life tables for Auke Creek Coho Salmon, created using individuals of known age and genotype that returned from 2013 to 2015. All age-3 males are pooled together (jacks and full-size males). Abundance (N_x), proportion (N_x/N), mean number of offspring produced (b_x), total number of offspring produced (B_x), and variance in number of offspring produced (V_x) are shown for each age class. For a stable population, the mean number of offspring produced (b'_x), total number of offspring produced (B'_x), and variance in number of offspring (V'_x) are noted with the prime symbol (').

Sex	Age Class	Age	N_x	N_x/N	b_x	B_x	V_x	b'_x	B'_x	V'_x
Female	1.1	3	209	0.16	0.53	111	1.95	2.21	463	26.92
	2.1	4	1061	0.84	0.55	585	1.66	2.30	2439	21.55
Male	1.0	2	26	0.02	0.19	5	0.32	0.80	21	3.02
	1.1	3	297	0.18	0.50	149	1.24	2.08	618	14.72
	2.0	3	443	0.27	0.26	116	0.53	1.09	481	5.75
	2.1	4	866	0.53	0.50	430	1.58	2.06	1783	20.72

GENERAL CONCLUSION

The aim of this research was to quantify the reproductive success of jacks, a common alternative life history form in Pacific salmon, and determine their influence on effective population size. To do this we used an extensive demographic and genetic dataset on Coho Salmon in the Auke Lake Drainage in Juneau, AK. Using parentage assignment, we found that jacks had lower reproductive success than full-size males. But even though jacks were less successful on a per-individual basis, they contributed substantially to the population. Additionally, jack presence generally increased the effective number of breeders although their contribution ranged widely. Reductions in N_b caused by removing jacks were primarily the result of the decrease in individuals but also the higher variance in full-size male reproductive success.

This study provides valuable information on jack life history and natural mating structure that will be useful for the conservation of Pacific salmon. We have shown that jacks can be successful and believe that ignoring jacks in studies could lead to faulty conclusions about population dynamics. If we had not included jacks in our analysis, we would have overestimated individual reproductive success and underestimated effective population size.

This research also has implications for hatchery programs. Currently, hatcheries in Southeast Alaska are not required to include jacks in their broodstock, and therefore most do not. In general, hatcheries mate pairs randomly, but since they exclude jacks, they are practicing selective mating. In some cases, hatcheries wishing to keep multiple of their broodlines separate will exclude jacks specifically for that purpose, because jacks returning at younger ages would mix broodlines. The results from this study suggest that excluding jacks from hatchery broodstock is a divergence from natural mating structure. The impact of this divergence on hatchery fish and natural fish is unknown. Including the same proportion of jacks in the hatchery as their proportion in the wild would not be truly representative either, because the relative reproductive success of jacks to full-size males was less than one. Building on the information in this study, investigations into the factors influencing jack contribution to effective population size in nature would help facilitate a clearer understanding of whether and to what proportion jacks should be included in hatchery broodstock.

Accounting for the presence of alternative life history strategies is essential when examining population viability and executing conservation programs. The benefits of life history variation on population persistence are well known. We demonstrated that the jack life history tactic influences population and evolutionary dynamics. We advise considering jacks while developing management plans for the conservation of Pacific salmon populations.