**Introduction**

The evolutionary history of Pacific salmon (*Oncorhynchus spp*.) is defined by a dynamic balance between disturbance, population connectivity and local adaptation (cite). Shifts in climate, marine productivity, sea level and geology have led to repeated extirpations, but also produced a mosaic of habitats and accompanying selective regimes on different temporal and spatial scales. Pacific salmon have evolved extensive life-history diversity under these conditions and successfully utilize a wide array of habitats throughout their range. Because productivity at broad scales (e.g. species, metapopulations, stocks) integrates asynchronous benefits and risks at fine scales (e.g. life-history variants, habitats), this diversity promotes stability and resilience in Pacific salmon (Brennan *et al.* 2019; Greene *et al.* 2010; Schindler *et al.* 2010). However, parallel impacts at broad temporal and spatial scales threaten the ability of this portfolio effect to buffer negative effects on Pacific salmon (Crozier *et al.* 2019; Waples *et al.* 2009).

For example, parallel effects of warming rivers caused by broad scale climate forcing, and reduced habitat connectivity caused by construction of passage barriers interact to reduce the resiliency of Chinook salmon (*Oncorhynchus tshawytscha*) (Cordoleani *et al.* 2021; FitzGerald *et al.* 2021; McClure *et al.* 2008; Munsch *et al.* 2022). Large dams (>15 m) have directly contributed to declines of Pacific salmon throughout their range by altering downstream temperature and flow regimes (Angilletta Jr *et al.* 2008; Crozier *et al.* 2020; Ligon *et al.* 1995; USAR 2021), creating reservoirs that delay migration and increase susceptibility to predation (High *et al.* 2006; Monzyk *et al.* 2015; Murphy *et al.* 2021; Schreck *et al.* 2006), and reducing overall productivity by truncating available freshwater habitat (sheer and steel 2006?). While, a variety of mechanisms have been employed to promote volitional upstream and downstream passage around dams, many dams are too high to support volitional passage. Impassible dams currently block access to X% of habitat in X particular basin, probably use sheer and steel 2006 (lost habitats). Importantly, the habitats beyond impassable dams are not evenly distributed, but are biased towards high-elevation tributaries (Sheer & Steel 2011)(other cites) that may serve as cold-water refugia during warm years (Ebersole *et al.* 2020; Myers *et al.* 2018), and are associated with particular life-history variants (Beechie *et al.* 2006)(other cites). Furthermore, life-history variation often has a heritable genetic basis (cites) and loss of habitat diversity may alter the abundance and evolutionary trajectories of life-history variants that may be critical to the evolutionary rescue of Chinook salmon (McClure *et al.* 2008)(better cite?). Therefore, while mitigation strategies, such as hatchery propagation below dams, may offset the direct impacts of dams by supplementing productivity, they cannot restore connectivity to the diverse habitats that is likely necessary for long term survival and abundance of Chinook salmon in a changing climate (Cordoleani *et al.* 2021; FitzGerald *et al.* 2021; Herbold *et al.* 2018). Ultimately, this connectivity can only come from reintroducing salmon into habitats above dams where they have been extirpated.

These constraints leave two options for communities wishing to retain the cultural, social and economic benefits of abundant Chinook salmon stocks: dam removal or trapping salmon and transporting them around dams using trucks or other means (hereafter trap-and-haul) (Lusardi & Moyle 2017). While removal of large dam is increasingly seen as feasible (O'Connor *et al.* 2015), and multiple recent dam removals have been successful in restoring connectivity and establishing populations above former barriers through natural recolonization (Allen *et al.* 2016; Duda *et al.* 2021; Hill *et al.* 2019), dam removal faces many socio-political hurdles because of the multiple social and economic benefits they provide. Even in the case of aging or low-benefit dams, significant costs, ecological tradeoffs and long timeframes may prevent their removal on conservation-relevant time scales (Stanley & Doyle 2003)(others).

Insert sentence about the wealth of knowledge possessed by trap-and-haul practitioners.

However, there are also significant challenges and uncertainties associated with trap-and-haul based reintroduction (Anderson *et al.* 2014; Kock *et al.* 2020; Lusardi & Moyle 2017). These challenges and uncertainties include risks of inbreeding and outbreeding depression (Huff *et al.* 2011; Huff *et al.* 2010), fitness costs of delayed migration (Dickerson *et al.* 2005; Marschall *et al.* 2011), phenotype-environment mismatches and imposition of artificial selection regimes (Evans *et al.* 2019; Tillotson *et al.* 2019), increased risks of pre-spawn mortality or disease susceptibility following handling and transport stress (Bowerman *et al.* 2018; Colvin *et al.* 2018; Keefer *et al.* 2010), and conflicts with extant populations, particularly source-sink dynamics (Pess *et al.* 2012; Sard *et al.* 2016b). Therefore, trap-and-haul programs must be frequently evaluated and adjusted using clearly defined metrics in an adaptive management framework (Anderson *et al.* 2014; Kock *et al.* 2020; Lusardi & Moyle 2017).

Trap-and-haul based reintroduction of spring Chinook salmon above impassible dams on several tributaries of the Upper Willamette River (Oregon, United States) has been ongoing for nearly three decades (cites). Reintroductions in the UWR are motivated/provide a variety of beneifts/motivations. These reintroductions have been subject to continuous and ongoing evaluation using multigenerational pedigrees inferred with genetic parentage analysis, permitting adaptive management (cites.) Evans 2016, Sharpe 2016, Weigel 2019. Importantly, inference of multigenerational pedigrees allows for adult recruits to be parsed into offspring of salmon previously released above the dam and immigrants produced elsewhere. This allows for the calculation of a cohort replacement rate (CRR), defined as “the number of future spawners produced by a spawner” (Botsford & Brittnacher 1998). A CRR greater than one suggests demographic viability without immigration, and net source dynamics for the reintroduced population. While a CRR less than one suggests the population is not demographically viable and is a net sink. These studies provide additional important insights into the reintroduction including estimates of genetic diversity, and the identification of management strategies that promote or reduce fitness.

In this study, we use genetic parentage analysis to evaluate a trap-and-haul based reintroduction above the Cougar Dam on the South Fork McKenzie River. Summary of previous results. We extend previous pedigrees to include insights into x years of adult returns and y years of reintroduced cohorts. We provide demographic information including estimates of productivty and fitness. The additional years of data improves the statistical power of our modeling approach used to evaluate trap-and-haul practices and identify significant predictors of fitness, with a particular focus on the relative reproductive success of hatchery-origin (HOR) *vs.* natural-origin (NOR) salmon reintroduced above the dam. We also examine a tag and release program used to manage the disposition of NOR salmon produced above or below the dam. Finally we discuss how our results can be used in to inform the adaptive management of the reintroduction program and also xxx applies to other reintros xxx.

* While hatchery supplementation attempts to compensate for lost productivity
  + Negative hatchery influence on wild stocks
  + Lower fitness
  + Cannot replace the diversity that promotes long term resilience. (Crozier overall, then, UWR (Myers *et al.* 2018) and California specifically (Herbold *et al.* 2018). Tasha paper?
* Removal is happening, and Elwha success story, but significant challenges (Quinones)

“ Our results showed that negative impacts of stream temperature warming can be offset for almost all ecotypes if formerly occupied habitat above dams is made available” (FitzGerald *et al.* 2021)

* Include history of construction in 1950s and 60s with trap-and-haul that were mostly abandoned and replaced with hatchery supplementation? (yes this is how evans and nuetzel structured it)

Adaptive variation is likely important to the success of species restoration efforts (56, 68), Given that spring-run Chinook have

historically been prominent on the southernmost edge of the

species range (26), the phenotype may carry substantial adaptive

importance for more northern locations under climate change (86).

* Dam removal and trap-and-haul based reintroductions are the only option to restore population connectivity and spatial diversity (and accompanying benefits).
* But must take place within an integrated, adaptive management framework, that includes habitat restoration, management of temperature and flow regimes, etc etc. For example source sink dynamics ()
* Downstream passage identified as the primary factor limiting productivity.

dams act to reduce longitudinal connectivity along rivers, importantly habitats beyond impassible barriers are biased towards (habitat characteristics from McClure 2008? Others?)

Dam removal is increasingly practiced as a river restoration tool to restore fish population sizes (O'Connor et al. 2015), but fewer than 10% of removed dams have been scientifically evaluated for their removal effectiveness on benefiting fish populations (Bellmore et al. 2017).

three sentence version of the intro im writing from Cordoleani:

Salmonids exhibit extensive phenotypic plasticity, which could

enhance population stability against disturbances by spreading risk

across time and space (portfolio effect concept12,21,22). However, multiple

concurrent environmental forcings could weaken this portfolio

effect and challenge species resilience to future climate change23.

In particular, the combination of warming and habitat contraction,

caused by dam construction, has resulted in large population

declines and erosion of salmon life history diversity, particularly for

runs that rely on cooler high-elevation habitats18,24

**Methods**

Study System

Spring Chinook salmon in the Upper Willamette River are listed as a threatened evolutionary significant unit (ESU) under the U.S. Endangered Species Act (ESA) (NMFS 1999). Construction and operation of multiple impassible dams throughout the Upper Willamette River have contributed to declines of this ESU (NMFS 2008). The McKenzie River, a tributary of the Upper Willamette River, historically supported one of the largest populations of spring Chinook salmon in the Willamette Basin (McElhany *et al.* 2007). Unlike most Upper Willamette River tributaries, the McKenzie River continues to produce a large proportion of natural-origin (NOR) spring Chinook salmon (Bowerman *et al.* 2018; Johnson & Friesen 2010). Access to historical spawning habitat on the McKenzie River is blocked by several dams. Construction of Cougar Dam (158m) in 1964 on the South Fork McKenzie River impeded access to approximately 40 river km of the historically most productive reaches on the river (NMFS 2008)(Figure 1).

Adult hatchery-origin (HOR) salmon collected from the McKenzie and Leaburg hatcheries on the McKenzie River have been released above Cougar Dam since 1993 (Figure 1). We refer to these individuals as *hatchery outplants*. The initial motivation for these releases was to re-establish historical ecosystem functions, including production of prey for ESA listed bull trout (*Salvelinus confluentus*) and transport of marine nutrients. However, anecdotal evidence suggested that offspring of hatchery outplants survived passage through Cougar Dam and returned to the South Fork McKenzie River as adults. A trap and haul facility was constructed at the base of Cougar Dam in 2010 (hereafter *the Cougar Trap*). The Cougar Trap has been operational throughout the spawning migration each year since 2010, except for July 19 to August 6,2011. The Cougar Trap collects NOR salmon produced above the dam and a small number of HOR salmon. Importantly, NOR salmon that are not produced above the dam also volitionally enter the Cougar Trap and are collected (hereafter *NOR immigrants*) (Banks *et al.* 2013; Banks *et al.* 2016; Banks *et al.* 2014; Sard *et al.* 2016b). Salmon collected at the trap are loaded in trucks and released above Cougar Dam at one of five sites to spawn (Figure 1). Supplementation of the above dam population with hatchery outplants from the McKenzie or Leaburg Hatcheries has continued since construction of the Cougar Trap. Genetic evidence has also confirmed that precocial resident males and adfluvial females make a small contribution to the productivity of the above dam population (Sard *et al.* 2016a). Therefore, spawners above Cougar dam are known to come from six sources: hatchery outplants, HOR salmon collected at the Cougar Trap, NOR salmon produced above the dam, NOR immigrants, precocial resident males, and adfluvial females.

Two programs have been implemented to manage the disposition of NOR salmon collected at the Cougar Trap, late-season downstream release (LSDR) and downstream recycling. Under LSDR all NOR Chinook salmon collected at the Cougar Trap after September 1 were double floy-tagged and released on the mainstem McKenzie River, downstream of the confluence with the South Fork McKenzie River (Figure 1). After September 1, only floy-tagged NOR Chinook salmon collected at the Cougar Trap were released above the dam. The LSDR program was implemented in 2013 and 2014 and reduced above dam transport of NOR immigrants relative to NOR salmon produced above the dam (Banks *et al.* 2016; Banks *et al.* 2014; Sard *et al.* 2016b). Downstream recycling has been implemented each year since 2015. Under downstream recycling, all NOR Chinook salmon collected at the Cougar Trap, regardless of date, are double floy-tagged and released into the mainstem, downstream of the confluence with the South Fork McKenzie River. Among NOR salmon collected at the Cougar Trap, only those with floy-tags are released above the dam.

To date, there is no assisted downstream passage for juveniles produced above the dam. Instead, juvenile fish can exit the reservoir volitionally, either by passage through hydroelectric turbines or over a steep, 73 m ‘regulating outlet’ spillway. Survival of downstream passage. Downstream passage survival identified as limiting factor. Indeed the CRR (a measure of population viability) has been less than one.

Sampling

Fin clips were taken from nearly all NOR Chinook salmon that entered the Cougar Trap from 2010 – 2015 and nearly all Chinook salmon released above the dam, regardless of origin, from 2007 – 2013 and used in previous evaluations of the reintroduction efforts above Cougar Dam (Banks *et al.* 2013; Banks *et al.* 2016; Banks *et al.* 2014; Sard *et al.* 2016b; Sard *et al.* 2015). We extended sampling to include fin clips from nearly all NOR Chinook salmon that entered the Cougar Trap from 2010 – 2020 and nearly all Chinook salmon released above the dam, regardless of origin, from 2007 – 2017. We also include fin clips collected from NOR Chinook salmon carcasses identified during spawning ground surveys (SGSs) on the South Fork McKenzie River from 2011 – 2019, including SGSs above the dam and SGSs between the confluence with the mainstem McKenzie River and the dam. Additionally, we include fin clips collected from precocial male Chinook salmon identified on spawning grounds above the dam during 2014.

Genetic Data

All NOR Chinook salmon sampled from 2016 – 2020, and all sampled Chinook salmon released above Cougar Dam from 2014 – 2017 were genotyped at a panel of microsatellite loci. Whole genomic DNA was isolated from fin clips using the protocol of Ivanova et al*.* (2006). Each DNA sample was then genotyped at 11 microsatellite loci: *Ots201*, *Ots208b, Ots209*, *Ots211*, *Ots212*, *Ots215*, *OtsG249*, *Ots253b, OtsG311*, *OtsG409*, *Ots515* (Banks *et al.* 1999; Greig *et al.* 2003; Naish & Park 2002; Williamson *et al.* 2002) and at the sex-linked marker, *Oty3*, to determine sex (Brunelli *et al.* 2008). Loci were amplified using polymerase chain reaction (PCR), PCR products were visualized on an ABI 3730xl DNA analyzer, and allele sizes scored using GENEMAPPER software (Version 5.0, Applied Biosystems, Inc., Foster City, CA). We also collated the unfiltered genotype data for all individuals that were genotyped in previous evaluations at the same microsatellite loci (Banks *et al.* 2013; Banks *et al.* 2016; Banks *et al.* 2014; Sard *et al.* 2016b; Sard *et al.* 2015), including all NOR Chinook salmon sampled from 2010 – 2015, and all sampled Chinook salmon released above Cougar Dam from 2007 – 2013. These data were appended to those collected for the present study before genotype quality filtering.

After genotype data collection and collation, we conducted genotype quality filtering and removed potential duplicates. Salmon with genotypes at less than seven loci were excluded, a threshold determined based on the sequential cumulative non-exclusion probabilities observed among loci. Multilocus genotypes were then compared among individuals to identify salmon that could have been sampled more than once. For example, NOR Chinook salmon sampled at the Cougar Trap might be later sampled as carcasses. We considered individuals first collected at the Cougar Trap and later sampled as carcasses during SGSs as Cougar Trap individuals in all subsequent analyses. If individuals failed to genotype at the sex-linked marker *Oty3*, phenotypic information was used to infer sex.

Genetic Parentage Analysis

Our objective was to evaluate the reintroduction of spring Chinook salmon above Cougar Dam. Therefore, when inferring pedigrees, we defined *potential offspring* as NOR Chinook salmon sampled anywhere on the South Fork McKenzie River and *candidate parents* as any Chinook salmon, regardless of origin, released or otherwise sampled above Cougar Dam (Figure 2). Potential offspring that did not assign to at least a single candidate parent were assumed to be *NOR immigrants* descended from parents that spawned in the South Fork McKenzie River below the dam, in the mainstem McKenzie River, or elsewhere.

Most Chinook salmon on the South Fork McKenzie River express an age at maturity of three to six years, with the majority being age-4 and age-5, and less than 2% age-6 (Banks *et al.* 2016). Therefore, we assigned potential offspring sampled on the South Fork McKenzie to candidate parents released above Cougar Dam three to six years prior. We assigned potential offspring that returned to the South Fork McKenzie River 2010 – 2020 to candidate parents released, or otherwise observed above the dam from 2007 – 2017 (Figure 2). Given the known age structure of returning adults, these assignments allow us to identify all offspring of salmon released above Cougar Dam from 2007 – 2014, most (likely >98%) offspring of salmon released above Cougar Dam in 2015, and some offspring of salmon released above the dam in 2016 and 2017 (Figure 3).

Genetic parentage analysis followed the approach used in previous studies evaluating spring Chinook salmon reintroductions throughout the Upper Willamette River (Banks *et al.* 2013; Banks *et al.* 2016; Banks *et al.* 2014; Evans *et al.* 2019; Evans *et al.* 2016; O’Malley *et al.* 2014; O’Malley *et al.* 2015; Sard *et al.* 2016b; Sard *et al.* 2015). Assignment of offspring to parents was first conducted within the maximum-likelihood framework of CERVUS v3.07 (Kalinowski *et al.* 2007). Then, we assigned parentage using the PLS-FL algorithm implemented in COLONY v2.0.6.8 (Jones & Wang 2010). We combined the outputs CERVUS and COLONY to generate a consensus pedigree used in all downstream analyses. Further detail of pedigree inference is available in the supplemental methods. We estimated non-exclusion probabilities and expected number of false parent-offspring pairs (Christie 2010) (supplemental table 1). We also estimated the allele miscall rate and dropout rate using COLONY (Wang 2018) (supplemental table 2).

Assignments

We summarized the number and proportion of unmarked adult Chinook salmon sampled at either the Cougar Trap or spawning grounds below Cougar Dam in 2010 – 2020 that can be assigned as offspring of Chinook salmon previously released above Cougar Dam in 2007 – 2017. To evaluate the effect of the LSDR and downstream recycling programs, we determined the number of both NOR salmon produced above the dam and NOR immigrants that were collected at the Cougar Trap each day. To better understand the relationship between arrival time at the Cougar Trap and the probability that a salmon was produced above the dam for offspring years 2013 – 2020 (when nearly all candidate parents are sampled), we fit a binomial generalized linear mixed model (GLMMimmigrant) using *sex*, and the *Julian day of sampling* at the Cougar Trap as predictors, *year* as a random intercept and a random slope for *Julian day of sampling*. Further detail of model selection, validation and hypothesis testing are provided in the supplemental methods.

Demography

We defined total lifetime fitness (TLF) as the total number of adult offspring assigned to a candidate parent (Figure 2). We analyzed candidate parents from 2007 – 2017 and potential offspring from 2010 – 2020. Therefore, we present TLF for candidate parents from 2007 – 2014. We also present partial estimates of TLF for candidate parents in 2015 (based on age-3, age-4, age-5 offspring only), 2016 (based on age-3, age-4, offspring only), and 2017 (based on age-3 offspring only) but note that these partial values underestimate TLF.

CRRswere estimated for each cohort of candidate parents released or observed above the Cougar Dam. We report CRRtotal, defined as the total number of offspring produced by salmon released or observed above Cougar Dam divided by the total number of salmon released or observed above Cougar Dam. We also report both a female-only CRRF and a male-only CRRM. For example, CRRF is the total number of female offspring produced by females released or observed above Cougar Dam divided by the total number of females released or observed above Cougar Dam. We present CRR estimates for parental cohorts from 2007 – 2015, but note that the 2015 CRR is likely an underestimate given that it does not include age-6 offspring.

The effective number of breeders (*Nb*) among cohorts of salmon released or observed above Cougar Dam was estimated using the linkage disequilibrium (LD) method, as implemented in the program NEESTIMATOR v2.1 (Do *et al.* 2014; Waples & Do 2008). This method examines patterns of LD (nonrandom allelic associations, which are suggestive of common ancestry) among offspring of a cohort. *Nb* was calculated using the genotypes of all offspring assigned to each parental cohort from 2007 – 2015. We excluded singletons and generated 95% confidence intervals using a jackknife re-sampling method (Waples and Do 2008).

Predictors of Fitness

We fit a generalized linear mixed model (GLMM) to identify significant predictors of fitness in the above dam population. Specifically, we fit a single GLMM on TLF of candidate parents from 2007 – 2014 and partial TLF of candidate parents from 2015, because age-6 offspring are expected to contribute very little to TLF (<2%) (hereafter GLMMTLF). We considered the influence of multiple potential predictors of fitness including *sex, origin, release day, release location, release group density, release group sex ratio, annual sex ratio.* In addition to fitting each of these predictors as a main fixed effect, we also examined three interaction terms, including *sex\*release day, sex\*origin,* and *sex\*annual sex ratio* and two random effects, *release group*, and *year. Release day* is the Julian day that individuals were released and was modeled as a continuous fixed effect. *Release group* is defined as the individuals released at a single location during a single day. *Release group density* is the number of individuals in a release group. *Release group sex ratio* is the ratio of males to females in a release group. *Annual sex ratio* is the ratio of males to females in a year. Sex ratios were log-transformed before inclusion as predictors in a model. Our modeling approach primarily followed the recommendations of Zuur et al. (2009) and Bolker (2015). Details of our modeling approach can be found in the supplemental methods.

We also fit a *post-hoc* GLMM on TLFfor a subset of candidate parents with *size at maturity* measurements (hereafter GLMMsize). We defined *size at maturity* as the fork length in cm for candidate parents measured at the time of release. This GLMMsize used the final significant predictors from the GLMM on TLF using all parents (GLMMTLF), but also included *size at maturity* as an additional fixed effect. Significance of the effect of *size at maturity* was tested using a likelihood ratio test. We also examined the relationship between *origin* and *size at maturity* using a linear mixed model that fit *size at maturity* as an effect of *origin, sex* and a random effect of year.

**Results**

Sampling and Genotyping

After filtering, there were 9839 individuals genotyped at an average of 10.86 microsatellite loci (Table 1). Ninety-nine percent of individuals in the filtered dataset were genotyped at nine or more loci. There were 6700 salmon initially collected at McKenzie or Leaburg Hatcheries and transported above Cougar Dam (hatchery outplants), 2930 NOR and HOR salmon initially encountered at the Cougar Trap and released above the dam or downstream, 12 precocial males sampled on spawning grounds above the dam, 192 carcasses sampled during SGSs below the dam, and five carcasses sampled during SGSs above the dam (Table 2).

Assignment

We attempted to assign 2915 potential offspring to 8985 candidate parents (Tables 4 and 3, respectively). Considering only the eight offspring years when all candidate parents that returned three to six years prior were sampled (2013 – 2020), 1183 of 1783 potential offspring assigned to at least one parent, for a total assignment rate of 67%. 1629 potential offspring were sampled at the Cougar Trap in this period. Of these 1629, 1151 assigned to at least one parent above Cougar Dam, for an assignment rate of 71%. Assuming individuals that did not assign to at least one parent above the dam were not produced above the dam, this suggests 29% of NOR salmon collected at the Cougar Trap were NOR immigrants. We found that the proportion of NOR immigrants collected at the Cougar Trap increased throughout the season (Table 5, Figure 4). In our model (GLMMimmigrant), the proportion of NOR immigrants collected at the Cougar Trap was estimated to increase from less than 5% early in the season to ~50% by September 1. However, there was substantial variation among years in the relationship between time and the proportion of NOR immigrants collected at the Cougar Trap. The 95% confidence interval of the predicted proportion of NOR immigrants on September 1 spanned from ~ 38% – 63%.

In 2015 – 2020, when downstream recycling was implemented, 875 NOR salmon collected at the Cougar Trap assigned to salmon released above the dam in 2009 – 2016. Of these 875 NOR salmon that were recycled downstream, 275 (31%) did not return to the trap, and 600 (69%) returned a second time. The mean interval between first and second collection at the Cougar Trap for these NOR salmon was 30.9 days (s.d. = 28.3). During the same period from 2015 – 2020, 334 NOR immigrants were collected at the trap. Of these, 252 (75%) did not return to the trap a second time, and 82 (25%) returned a second time. In summary, NOR salmon produced above the dam were significantly more likely to return a second time than NOR immigrants (odds ratio = 6.7, Fisher’s exact test, p = 2.2 x 10-16). If LSDR using a September 1 cutoff date had been implemented during these years instead of downstream recycling, 834 (95%) NOR salmon produced above the dam and 212 (63%) NOR immigrants would have been released above the dam.

Demography

*Age at Maturity*

Among the years when we could identify age-3 through age-6 salmon (2013 – 2020), most salmon were age-4 or age-5 (54.6% and 42.0%, respectively), with few returning at age-3 or age-6 (1.6% and 1.8%, respectively). This pattern was consistent across all years, however, there was substantial variation in the proportion of age-4 and age-5 returns from year to year (Figure 5).

*Total Lifetime Fitness*

We present the mean TLF for candidate parents as well as its range and standard deviation by year, sex, and origin in Table 6. From 2007 – 2015, there were 7453 candidate parents, and only 1511 (20%) produced at least one offspring that returned to the Cougar Trap or was sampled as a carcass below the dam. For the parental cohort years when all (2007 – 2014) or most (2015) offspring are expected to have returned, the overall mean TLF was 0.36 and ranged from 0 – 17. For the subset of these years when both NOR and HOR salmon were released above the dam (2010 – 2015), mean TLF was greater for NOR than HOR salmon (0.49 *vs.* 0.23, respectively).

*Cohort Replacement Rate*

The total cohort replacement rate (CRRtotal) was less than one in all years from 2007 – 2015, indicating that the population above Cougar Dam is not replacing itself (Table 7). Maximum CRRtotal (0.44) was observed in 2007, and minimum CRRtotal (0.08) was observed in 2009, both years when only HOR hatchery outplants were released above the dam. In most years (2007 – 2012), females were the limiting sex. CRRF was less than one in these years. In the three years when males were the limiting sex (2013 – 2015), CRRM was also less than one.

*Effective Number of Breeders*

The effective number of breeders (*Nb*), ranged from 139.8 to 368.8 (Table 8), indicating that there is likely sufficient genetic diversity within a cohort to avoid inbreeding depression. The ratio of *Nb* to the number of candidate parents ranged from 0.22 to 0.36.

Predictors of Fitness

*Generalized Linear Mixed Modeling*

We did not find evidence of strong multicollinearity among the evaluated predictors of TLF (GVIF1/2\*df < 2), and included all predictors at the start of model selection. Modeling the effect of *release group density* as a second order polynomial provided a marginally better fit to the data than modeling *release group density* as a linear predictor, but all other predictors were modeled as linear effects. The best random effects structure according to AIC included random intercepts for both *year* and *release group.* After model selection of fixed effects, four predictors and two interactions were included in the final model: *sex, origin, Julian day of release, annual sex ratio*, *sex\*origin* and *sex\*annual sex ratio.* Parameter estimates and their standard errors, as well as significance testing for each predictor retained in the final model are presentedin Table 9*.*

*Effects of Significant Predictors of TLF*

To aid in interpretation of the parameters estimated in the final model (Table 9), we also estimated effects of each significant predictor on the response scale (TLF) after accounting for variation at all other significant predictors (Figures 7 – 9). NOR salmon have substantially higher predicted fitness than HOR salmon and this effect is somewhat stronger for males than females, but this interaction is only marginally significant and has a limited effect size (Figure 7). NOR males are predicted to be 2.1-fold more fit than HOR males, and NOR females are predicted to be 1.6-fold more fit than HOR females. Overall, the *annual sex ratio* has a small, and marginally significant effect on TLF, with male-biased sex ratios producing somewhat higher fitness than female-biased sex ratios, however this effect was much stronger for females than males. When viewed on response scale (TLF) (Figure 8), changes in *annual sex ratio* affects fitness mostly through females, who perform worse when the sex ratio is female-biased. Using the most extreme values observed in any years (male:female ratio 0.6 and 2.0), female fitness is predicted to vary 3.5-fold, whereas male fitness is expected to vary 1.4-fold. Finally, salmon released above Cougar Dam earlier in the season are predicted to have greater fitness than those released later (Figure 9). Individuals released on the earliest day in the dataset are predicted to have 1.7-fold greater fitness than the latest release day.

The random effects of *year* and *release group* also contribute substantially to the variation in TLF among individuals (Table 9). Variation in TLF attributed to differences among years or release groups, as measured by standard deviation of the *year* and *release group* random effects, was similar in scale to the fixed effect of *origin* presented above*.*

*Size at Maturity*

Our dataset included *size at maturity* for approximately one half of the candidate parents released above the dam from 2007 – 2015 used to fit GLMMTLF. NOR salmon released above the dam were significantly larger than their HOR counterparts after controlling for size differences owing to *sex* and *year* (linear mixed model, βorigin [NOR] = 2.92 cm, s.e. = 0.26, p-value likelihood ratio test < 2.2 x 10-16). To evaluate the relationship between *size at maturity*, *origin* and TLF, we fit a GLMM on TLF for the 3781 candidate parents with a *size at maturity* measurement, using the significant predictors of fitness from the final model and *size at maturity* as an additional predictor (GLMMsize). Size had a significant positive effect on TLF (βsize = 0.069, s.e. = 0.006, p-value likelihood ratio test < 2.0 x 10-16), and the estimated effect of origin was reduced to 44% of its estimated effect when *size at maturity* was not included in the model, confirming that these two variables are highly confounded.

**Discussion**

* Diversity: Nb greater than 50, threshold established to address concerns around inbreeding (Waples 1990)
* Citations in the Kock review highlight how trap and haul delays migration with assumed negative impacts on fitness. We actually quantify this fitness effect. LSDR/DR associated with average delay of migration of x days, and this delay is associated with XXX% loss of fitness . “early migrating adult phenotypes that arrive late on spawning grounds may have reduced reproductive opportunity and decreased lifetime fitness (e.g., Dickerson et al. 2005 ).”, however,
* Our analysis of the NOR immigrants illustrates the importance of monitoring, and highlights how adaptive management must take source-sink dynamics into account.

**Tables**

**Table 1.** Summary of genotype quality filtering. Individuals were removed from the analysis if they were genotyped at < 7 loci (missingness filtered), or if they represented a duplicate multilocus genotype (duplicate filtered).

\* Indicates some or all individuals from this year were genotyped in prior reports

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Year** | **Tissue Samples** | **Missingness Filtered** | **Duplicate Filtered** | **Nfinal** |
| 2007\* | 746 | 1 | 0 | 745 |
| 2008\* | 873 | 0 | 0 | 873 |
| 2009\* | 1386 | 2 | 1 | 1383 |
| 2010\* | 748 | 1 | 0 | 747 |
| 2011\* | 791 | 20 | 1 | 770 |
| 2012\* | 962 | 3 | 2 | 957 |
| 2013\* | 695 | 4 | 1 | 690 |
| 2014\* | 744 | 16 | 2 | 726 |
| 2015\* | 917 | 28 | 5 | 884 |
| 2016 | 891 | 20 | 4 | 867 |
| 2017 | 718 | 9 | 2 | 707 |
| 2018 | 156 | 1 | 0 | 155 |
| 2019 | 192 | 18 | 1 | 173 |
| 2020 | 169 | 7 | 0 | 162 |

**Table 2.** Sample sizes after genotype quality filtering of salmon initially encountered at McKenzie or Leaburg Hatcheries (hatchery outplant), at the Cougar Trap, during spawning ground surveys (SGS) above or below Cougar Dam, or as precocial males observed on the spawning grounds above Cougar Dam. Note that all hatchery outplants are HOR, Cougar Trap salmon include both NOR, HOR and unknown origin salmon, and all precocial males and SGS salmon are NOR.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Year** | **Hatchery Outplant** | **Cougar Trap** | | | **Precocial Male** | **SGS** | |
|  |  | HOR | NOR | Unknown |  | Below | Above |
| 2007 | 745 |  |  |  |  |  |  |
| 2008 | 873 |  |  |  |  |  |  |
| 2009 | 1383 |  |  |  |  |  |  |
| 2010 | 496 | 30 | 221 |  |  |  |  |
| 2011 | 340 | 29 | 356 |  |  | 45 |  |
| 2012 | 430 | 17 | 500 |  |  | 10 |  |
| 2013 | 440 | 22 | 223 |  |  | 5 |  |
| 2014 | 486 | 21 | 191 | 1 | 12 | 14 | 1 |
| 2015 | 600 | 19 | 241 |  |  | 24 |  |
| 2016 | 459 | 74 | 295 | 4 |  | 31 | 4 |
| 2017 | 448 | 6 | 239 | 1 |  | 13 |  |
| 2018 |  |  | 120 |  |  | 35 |  |
| 2019 |  |  | 158 |  |  | 15 |  |
| 2020 |  |  | 162 |  |  |  |  |

**Table 3.** Number of individuals released or otherwise sampled above Cougar Dam retained in the final filtered dataset. These values correspond to candidate parents used in genetic parentage analysis. All hatchery outplants are HOR, all precocial males and SGS individuals are NOR.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Year** | **Hatchery Outplant** | **Cougar Trap** | | | **Precocial Male** | | **SGS** |
|  |  | HOR | NOR | Unknown | |  |  |
| 2007 | 745 |  |  |  | |  |  |
| 2008 | 873 |  |  |  | |  |  |
| 2009 | 1383 |  |  |  | |  |  |
| 2010 | 496 | 30 | 221 |  | |  |  |
| 2011 | 340 | 29 | 356 |  | |  |  |
| 2012 | 430 | 17 | 500 |  | |  |  |
| 2013 | 440 | 15 | 172 |  | |  |  |
| 2014 | 486 | 20 | 132 | 1 | | 12 | 1 |
| 2015 | 600 | 19 | 135 |  | |  |  |
| 2016 | 459 | 70 | 171 | 1 | |  | 4 |
| 2017 | 448 | 5 | 151 | 1 | |  |  |

**Table 4.** Number of NOR Chinook salmon sampled in the South Fork McKenzie River and retained after genotype quality filtering (*npotential offspring*) in each year and the number (*nassigne****d***) and percent (% Assigned) assigned to candidate parents. Results for the full set of potential offspring including those sampled at the Cougar Trap, during spawning ground surveys or as precocial males above the dam (Overall), and potential offspring initially sampled at the Cougar Trap only (Cougar Trap) are presented separately. Note that the percent of NOR immigrants is equal to (1 - % assigned) for the Cougar Trap in 2013 – 2020.

\* Note that for potential offspring that returned in 2010 – 2012, not all candidate parents are included in the genetic parentage analysis.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Overall** | | |  | **Cougar Trap** | | | |
| **Year** | ***npotential offspring*** | ***nassigned*** | **% Assigned** |  | ***npotential offspring*** | | ***nassigned*** | **% Assigned** |
| 2010\* | 221 | 14 | 6% |  | 221 | 14 | | 6% |
| 2011\* | 401 | 140 | 35% |  | 356 | 138 | | 39% |
| 2012\* | 510 | 328 | 64% |  | 500 | 326 | | 65% |
| 2013 | 228 | 153 | 67% |  | 223 | 153 | | 69% |
| 2014 | 218 | 118 | 54% |  | 191 | 117 | | 61% |
| 2015 | 265 | 179 | 68% |  | 241 | 176 | | 73% |
| 2016 | 330 | 228 | 69% |  | 295 | 212 | | 72% |
| 2017 | 252 | 173 | 69% |  | 239 | 169 | | 71% |
| 2018 | 155 | 100 | 65% |  | 120 | 92 | | 77% |
| 2019 | 173 | 84 | 49% |  | 158 | 80 | | 51% |
| 2020 | 162 | 152 | 94% |  | 162 | 152 | | 94% |

**Table 5.** GLMMimmigrant model fit. Results of generalized linear mixed model examining the influence of *sex, Julian day of sampling* on whether an NOR salmon sampled at the Cougar Trap was assigned to at least one parent from above the dam. Only the first observation of an individual is used. Estimated effect (β) and standard error (s.e.) of each fixed predictor on the link (logit) scale for predictors that were retained in the final model are presented. Variance (σ2) and standard deviation (s.d.) for random intercepts for year and random slope *Julian day of sampling* per year and their correlation (ρ) are also presented. The null hypothesis that each predictor did not significantly improve the model effect was tested with a likelihood ratio test (LRT p-value). The null hypothesis that each predictor has an effect significantly different than zero was evaluated with the Wald test (Wald p-value). Significant p-values are in bold.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Fixed Effects** | **β** | **s.e.** | **LRT**  **p-value** | **Wald**  **p-value** |
| (Intercept) | 7.130 | 0.930 |  | **1.7 x 10-14** |
| *Julian day of sampling* | -0.029 | 0.004 | **4.7 x 10-5** | **1.3 x 10-12** |
| *Sex*[Male] | -0.261 | 0.135 | 0.053 | 0.054 |
| **Random Effects** | **σ2** | **s.d.** | **ρ** |  |
| *year*(Intercept) | 4.883 | 2.209 | -0.95 |  |
| *year \* Julian day of sampling* | 8.5 x 10-5 | 0.009 |  |  |

**Table 7.** Cohort Replacement Rate (CRRtotal) per parent year. CRRtotal was estimated by determining the number of offspring successfully assigned to at least one parent in a given year (noffspring) and dividing it by the number of candidate parents (ncand) in that year. We also present CRRF: the number female offspring successfully assigned to at least one female parent in a given year, divided by the number of female candidate parents (ncand female) in that year. CRRM is the equivalent value for males.  
\* Note that 2015 estimates do not include potential age-6 offspring. However, we expect these offspring to contribute very little to TLF (~2%).

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Year** | ***noffspring*** | ***ncand*** | ***ncand male*** | ***ncand female*** | **Sex Ratio (male:female)** | **CRRtotal** | **CRRF** | **CRRM** |
| 2007 | 331 | 745 | 427 | 318 | 1.3 : 1.0 | 0.44 | 0.36 | 0.43 |
| 2008 | 247 | 873 | 585 | 288 | 2.0 : 1.0 | 0.28 | 0.30 | 0.26 |
| 2009 | 114 | 1383 | 780 | 603 | 1.3 : 1.0 | 0.08 | 0.06 | 0.08 |
| 2010 | 94 | 747 | 484 | 263 | 1.8 : 1.0 | 0.13 | 0.12 | 0.11 |
| 2011 | 284 | 725 | 405 | 320 | 1.3 : 1.0 | 0.39 | 0.34 | 0.32 |
| 2012 | 171 | 947 | 508 | 439 | 1.2 : 1.0 | 0.18 | 0.11 | 0.19 |
| 2013 | 151 | 627 | 302 | 325 | 1.0 : 1.1 | 0.24 | 0.14 | 0.26 |
| 2014 | 73 | 652 | 266 | 386 | 1.0 : 1.5 | 0.11 | 0.08 | 0.11 |
| 2015\* | 69 | 754 | 289 | 465 | 1.0 : 1.6 | 0.09 | 0.06 | 0.12 |

**Table 8.** Effective number of breeders (*Nb*) per parent year as estimated by NeEstimator v2.1. Number of candidate parents (*ncand*) is the number of salmon sampled, released above the Cougar Dam in a given year and successfully genotyped. *nsuccess* is the number of candidate parents with one or more offspring in the pedigree. *noffspring* is the number of offspring assigned to candidate parents released above the dam that parent year. Upper and lower 95% confidence intervals based on jack-knife are provided. The *Nb* : *ncand* ratiois provided for each year.

\* Note that 2015 estimates do not include potential age-6 offspring. However, we expect these offspring to contribute very little to TLF (~2%)

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Year** | ***ncand*** | *nsuccess* | ***noffspring*** | ***Nb*** | **CIlower** | **CIupper** | ***Nb* : ncand ratio** |
| 2007 | 745 | 261 | 331 | 265.5 | 222.7 | 322.8 | 0.36 |
| 2008 | 873 | 229 | 247 | 247.5 | 203.7 | 308.8 | 0.28 |
| 2009 | 1383 | 156 | 114 | 368.6 | 228.1 | 848.6 | 0.27 |
| 2010 | 747 | 105 | 94 | 169.8 | 116.6 | 288 | 0.23 |
| 2011 | 725 | 209 | 284 | 220.1 | 181.7 | 272.7 | 0.30 |
| 2012 | 947 | 206 | 171 | 297.2 | 216.5 | 451.4 | 0.31 |
| 2013 | 627 | 152 | 151 | 139.8 | 104.3 | 199.7 | 0.22 |
| 2014 | 652 | 90 | 73 | 167.5 | 104.7 | 361.6 | 0.26 |
| 2015\* | 754 | 103 | 69 | 211.9 | 122.1 | 627.5 | 0.28 |

**Table 9.** Results of generalized linear mixed model examining the influence of *sex, origin, release day, release location, release group density, release group sex ratio, annual sex ratio,* *sex\*release group density,* *sex\*release day, sex\*origin, and sex\*annual sex ratio* on the total lifetime fitness of spring Chinook salmon released above Cougar Dam from 2007 – 2015. *Year* and *release group* are included as random effects. Estimated effect (β) and standard error (s.e.) of each fixed predictor on the link (log) scale for predictors that were retained in the final model are presented above. The null hypothesis that each predictor did not significantly improve the model effect was tested with a likelihood ratio test (LRT p-value). The null hypothesis that each predictor has an effect significantly different than zero was evaluated with the Wald test (Wald p-value). Estimated variance (σ2) and standard deviation (s.d.) are presented for random effects. Significant p-values are in bold.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Fixed Effects** | **β** | **s.e.** | **LRT**  **p-value** | **Wald**  **p-value** |
| (Intercept) | -1.343 | 0.208 |  |  |
| *sex* [male] | -0.150 | 0.082 |  | 0.066 |
| *origin* [NOR] | 0.446 | 0.132 |  | **0.001** |
| *Julian day of release* | -0.004 | 0.001 | **0.004** | **0.003** |
| *annual sex ratio* | 1.042 | 0.501 |  | **0.038** |
| *sex* [male] \* *origin* [NOR] | 0.293 | 0.142 | **0.039** | **0.039** |
| *sex* [male] \* *annual sex ratio* | -0.750 | 0.177 | **<0.001** | **<0.001** |
| **Random Effects** | **σ2** | **s.d.** |  |  |
| *year* | 0.306 | 0.553 |  |  |
| *release group* | 0.085 | 0.292 |  |  |

**Table 6.** Mean TLF, standard deviation (s.d.) and range per parent year, sex, and origin.

\* Note that 2015 estimates do not include potential age-6 offspring. However, we expect these offspring to contribute very little to TLF (~ 2%).

\*\* Note that 2016 and 2017 estimates do not include age-5 and age-6 offspring, and age-4, age-5, and age-6 offspring, respectively, which are expected to contribute substantially to TLF for these parents’ years.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Year** | **Sex** | **HOR** | | | |  | **NOR** | | | |
|  |  | *n* | Mean | s.d. | Range |  | *n* | Mean | s.d. | range |
| 2007 | F | 318 | 0.89 | 1.49 | 0 - 11 |  |  |  |  |  |
|  | M | 427 | 0.72 | 1.56 | 0 - 17 |  |  |  |  |  |
| 2008 | F | 288 | 0.80 | 1.46 | 0 - 12 |  |  |  |  |  |
|  | M | 585 | 0.40 | 1.03 | 0 - 9 |  |  |  |  |  |
| 2009 | F | 603 | 0.16 | 0.47 | 0 - 4 |  |  |  |  |  |
|  | M | 780 | 0.13 | 0.43 | 0 - 3 |  |  |  |  |  |
| 2010 | F | 206 | 0.29 | 0.73 | 0 - 5 |  | 57 | 0.25 | 0.63 | 0 - 3 |
|  | M | 320 | 0.13 | 0.52 | 0 - 6 |  | 164 | 0.29 | 0.69 | 0 - 4 |
| 2011 | F | 176 | 0.76 | 1.57 | 0 - 9 |  | 144 | 0.68 | 1.33 | 0 - 7 |
|  | M | 193 | 0.27 | 0.69 | 0 - 4 |  | 212 | 0.86 | 1.74 | 0 - 9 |
| 2012 | F | 256 | 0.25 | 0.58 | 0 - 3 |  | 183 | 0.41 | 0.77 | 0 - 5 |
|  | M | 191 | 0.18 | 0.46 | 0 - 2 |  | 317 | 0.37 | 0.78 | 0 - 5 |
| 2013 | F | 248 | 0.28 | 0.7 | 0 - 5 |  | 77 | 0.75 | 1.25 | 0 - 6 |
|  | M | 207 | 0.21 | 0.56 | 0 - 3 |  | 95 | 0.85 | 1.41 | 0 - 8 |
| 2014 | F | 334 | 0.14 | 0.45 | 0 - 3 |  | 52 | 0.27 | 0.79 | 0 - 4 |
|  | M | 172 | 0.23 | 0.57 | 0 - 3 |  | 80 | 0.30 | 0.72 | 0 - 3 |
| 2015\* | F | 417 | 0.12 | 0.35 | 0 - 2 |  | 48 | 0.31 | 0.95 | 0 - 6 |
|  | M | 202 | 0.17 | 0.50 | 0 - 4 |  | 87 | 0.31 | 0.58 | 0 - 3 |
| 2016\*\* | F | 336 | 0.3 | 0.64 | 0 - 5 |  | 64 | 0.39 | 0.63 | 0 - 2 |
|  | M | 193 | 0.35 | 0.84 | 0 - 6 |  | 107 | 0.54 | 1.16 | 0 - 8 |
| 2017\*\* | F | 328 | 0 | 0 | 0 - 0 |  | 42 | 0 | 0 | 0 - 0 |
|  | M | 125 | 0 | 0 | 0 - 0 |  | 109 | 0 | 0 | 0 - 0 |

**Figures**

Map

Description automatically generated

**Figure. 1.** Map of McKenzie River watershed, including major dams (gold squares), hatcheries (green circles), and release sites on the mainstem (pink circle) and on the South Fork McKenzie River, above Cougar Dam (purple circles). Data sources: ESRI World Hillshade, USGS NHDPlus HR

A picture containing diagram

Description automatically generated

**Figure 2.** Illustration of genetic parentage analysis. Groups of individuals are organized into sets of potential offspring (solid rectangle) and candidate parents (dashed rectangle). Here, the 205 potential offspring that returned to the South Fork McKenzie in 2014 are assigned to 3728 candidate parents released above Cougar Dam three to six years earlier (2008 – 2011). Source refers to where an individual was initially encountered: during a spawning ground survey on the South Fork McKenzie River (SGS), at the Cougar Trap (Cougar Trap) or at either the McKenzie Hatchery or Leaburg Hatchery (hatchery outplant). Final location refers to whether a salmon was released above Cougar Dam (above) or not (below). Potential offspring include all NOR salmon, regardless of source or final location. Candidate parents include all salmon released above the dam, regardless of origin or source.

\* Note that five NOR SGS individuals and 12 NOR precocial males sampled above Cougar Dam are also included as both candidate parents and potential offspring and are not depicted in the figure.

A picture containing graphical user interface

Description automatically generated

**Figure 3.** Illustration of how genetic parentage analysis results (Figure 2) are combined to make demographic inferences about parental cohorts. Here we demonstrate how inferences about the 2013 parental cohort are drawn. Assignments of offspring in 2016 – 2019 (solid rectangle) to parents in 2013 (dashed rectangle) are depicted as black arrows. Labels are as in Figure 2 except the values inside circles which now reflect the number of candidate parents and assigned offspring. For example, total cohort replacement rate is the sum of the values in the solid rectangle divided by the sum of the values in the dashed rectangle.

Chart, line chart

Description automatically generated

**Figure 4.** Effect of *Julian day of sampling* on the predicted proportion of NOR salmon collected at the Cougar Trap was produced above the dam (thick black line) as predicted by GLMMimmigrant. Only the first observation of a salmon at the Cougar Trap was used. Vertical dashed red line indicates Julian Day 245, which corresponds to either September 1 or October 31, depending on the year. Light colored lines and confidence intervals show predicted effect of *Julian day of sampling* from separate binomial GLMs fit to data from each year.

Chart

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**Figure 5.** Inferred age at maturity for NOR salmon sampled in South Fork McKenzie River from 2010 – 2020.

\* Parents prior to 2007 are not included as candidate parents in the genetic parentage analysis. Therefore, offspring in years 2010, 2011, and 2012 cannot be identified across the full range of potential ages.

Chart, line chart

Description automatically generated

**Figure 6.** Mean Total Lifetime Fitness (TLF) and standard deviation from 2007 – 2015, by sex and origin.

\* Note that 2015 TLF estimates do not include potential age-6 offspring. However, we expect these offspring to contribute very little to TLF (~2%).

Chart, box and whisker chart

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**Figure 7.** Predicted effects of *origin* (NOR *vs.* HOR) and *sex* on TLF from GLMMTLF. Predicted values are conditioned on the typical values of all other predictors in the final model (*Julian day of release, annual sex ratio*). Error bars depict 95% confidence intervals for the estimates.

Chart, histogram

Description automatically generated

**Figure 8.** Predicted effects of *annual sex ratio* and *sex* on TLF from GLMMTLF. Predicted values are conditioned on the typical values of all other predictors in the final model (*Julian day of release, origin*). Rug plot at bottom of the figure highlights the observed *annual sex ratios* used to fit the model. Bands represent 95% confidence intervals for the estimates.

Chart, line chart

Description automatically generated

**Figure 9.** Predicted effects of *Julian day of release* on TLF from GLMMTLF. Predicted values are conditioned on the typical values of all other predictors in the final model (*Julian sex, origin, annual sex ratio*). Grey band represents 95% confidence intervals for the estimates.

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