Salmon Life Histories and Fisheries Management

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Abstract

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Understanding the life histories of exploited aquatic taxa is important to sustainable fisheries management. Life history diversity has been shown to stabilize population dynamics through ‘portfolio effects’ which can maintain robust fishery yields despite environmental variability. Moreover, the reproductive life histories of fishes can be important to shaping management-relevant properties such as the steepness of the stock-recruit relationship, genetic diversity, age and size structure, and stock rebuilding potential. Despite the importance of life history information to conservation and management, achieving a practical understanding of the evolutionary and ecological factors that maintain particular life histories can be challenging. This difficulty is exemplified by widespread declines in size-and-age-at-maturity of many commercially valuable fish stocks, the causes of which are seldom be reliably discerned. In this dissertation, I seek to better understand the factors that control the frequencies of alternative maturation and reproductive life histories in sockeye salmon (*Oncorhynchus nerka*) populations.

In chapter 1, I used Bayesian hierarchical modelling to identify the basis of variation in early maturation rates among sockeye salmon populations in Bristol Bay, Alaska. In my second chapter, I developed an age-structured Bayesian state space model to assess the causes of elevated early maturation rates in Kodiak sockeye salmon. Finally, in my third chapter I developed an individual-based population dynamics framework to explore the ecological and evolutionary factors that regulate frequencies of alternative maturation and reproductive life histories in age-structured populations. Collectively, my results demonstrate that the maintenance of alternative life histories within populations may be more complex than existing evolutionary frameworks suggest, and reveal a novel role of population dynamics in the evolution and maintenance of complex mating systems.

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so grateful to each of you for your mentorship and genuine investment in my research and education.

I have also been fortunate to work with several long-term data sets that reflect the hard work of many people. Jackie Carter, and the many past students and staff (anyone who ever picked through a rotting salmon brain looking for ear bones) of the Alaska Salmon Program helped collect the extraordinary age composition dataset that made my first chapter possible. Similarly, George Pess designed the protocol and collected much of the stream geomorphology data that I used in my first chapter. When I needed to replicate his protocol to sample new locations, he generously volunteered his time to come to Alaska and not only taught me how, but helped me complete all of the remaining surveys.

The core questions in this dissertation arose from puzzling observations of high jack levels in the Frazer Lake sockeye salmon population on Kodiak Island that were first described by members of the Alaska Department of Fish and Game, Kevin Schaberg and M. Birch Foster. Kevin and Birch have each been tremendously helpful in sharing their understanding of Kodiak's salmon fisheries and habitats with me, and this research would not have been possible without them. I would also like to thank both Kevin and Birch, as well as Darin Ruhl, Bill Kane, and Mary Hostetter for hosting me on my visits to Kodiak and the Frazer fish pass. My trips to Kodiak were among the most memorable and enjoyable experiences I have had in graduate school, and it would not have been possible without them. I would also like to thank the entirety of the Alaska Department of Fish and Game, as well as the Department of Fisheries and Oceans, Canada for collecting and generously sharing the long-term monitoring data that made my second and third chapters possible.

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DEDICATION

The work herein is dedicated to Katherine DeFilippo.

GENERAL INTRODUCTION

In his 1992 Robert H. MacArthur Award Lecture, Simon A. Levin wrote: "*the chasm between evolutionary biology and ecosystem science is a wide one, and there is little overlap between the two in journals or scientific meetings. Yet neither discipline can afford to ignore the other: evolutionary changes take place within the context of ecosystems, and an evolutionary perspective is critical for understanding organisms' behavioral and physiological responses to environmental change"*. Nearly 30 years later, Levin (1992)'s assertions take on renewed importance today as climate change is rapidly altering the structure and function of ecosystems across the globe (Walther 2010), and scientists are increasingly charged with pursuing 'ecosystem-based' approaches to natural resource management (Crowder et al. 2008). It has become clear that evolutionary change can occur over contemporary time scales, such that understanding interactions between ecological and evolutionary processes is often critical to understanding the realized behavior of populations (Stockwell, Hendry, & Kinnison, 2003). For instance, investigations of climate change impacts on animal populations have shown both ecological and demographic responses (*e.g.* distribution shifts, Pinksy Worm, Fogarty, Sarmiento, & Levin, 2013), as well as evolutionary changes (*e.g.* Skelly et al. 2007).

Perhaps one of the most important applications of evolutionary ecology to a changing world is understanding the factors that regulate species' life histories. An organism's life history strategy can be broadly defined as its pattern of life cycle events (*e.g.* birth, growth and development, maturation, reproduction *etc.*) and allocation tradeoffs (*e.g.* growth versus reproduction, offspring quantity versus quality *etc.*) which have evolved through natural selection. Species' life histories can have important ramifications for their ecology and management, as life history diversity has been shown to stabilize population dynamics in the face of environmental variability (Schindler et al 2010), and life history characteristics underly many of the vital rates that shape a population's response to harvest and environmental disturbances (He, Mangel, & MacCall, 2006; Munyandorero, 2020).

Teleost fishes are characterized by substantial life history diversity. In particular, fishes exhibit an astounding diversity of reproductive life histories, both among and within species (Taborsky 2008). The latter, often referred to as 'alternative reproductive tactics (ARTs)' represent a special case of life history variation that is defined by discrete categories rather than continuous phenotypic variation distributed around a single optimum (Shuster & Wade, 2003; Taborsky, Oliveira, & Brockmann, 2008). The coexistence of such discrete alternative phenotypes within a population is inconsistent with classical evolutionary models predicated on optimization principles (Schaffer, 1997; Stearns, 1980). As such, researchers often take a game theoretic approachto the study of life history evolution, in which the fitness of individuals may depend on the phenotypic expression of others in the population (Maynard Smith, 1982). Perhaps the most well-known example of such a mechanism is negative frequency-dependent selection (FDS) (Ayala and Campbell 1973). By reducing the fitness of any single life history variant as it becomes more common, negative FDS is thought to stabilize the coexistence of multiple alternative phenotypes in a population. However, predictions from FDS and related frameworks implicitly assume a population that is at equilibrium, while many fish populations exhibit large and often unpredictable fluctuations in abundance that violate the core assumptions of equilibrium population dynamics (Hilborn and Walters 1992).

In this dissertation, I seek to better understand how population dynamics interact with evolutionary processes to shape the evolution and maintenance of alternative life histories in animal populations. In addressing this broad question, I focus primarily on a single species:

sockeye salmon (*Oncorhynchus nerka*). Like several other species of salmon, sockeye exhibit a mating system composed of 'hooknose males' which spend multiple years at sea, attain a large body size, and attempt to mate with females through direct courtship and intrasexual contests, and 'jacks' which return from sea a year before the youngest females in the population and attempt to mate through 'sneaking' (Quinn 2005). Empirical and theoretical studies suggest that alternative male life histories in salmon are subject to frequency dependent selection (Berejikian et al., 2010; Gross, 1984, 1985; Hutchings & Myers, 1994). However, several studies have challenged the feasibility of a stable evolutionary equilibrium in the presence of persistent stochastic variability in growth and survival (Koseki & Fleming, 2006; Koseki & Fleming, 2007). Moreover, some salmon populations have exhibited large increases in the prevalence of jacks, degrading fishery yields and posing a difficult management challenge with no clear solution (Ford, Murdoch and Howard 2012).

Here, I present three chapters to investigate how alternative male life histories are maintained in sockeye salmon populations, and evaluate implications for fisheries. In Chapter One, I examine the basis of variation in male life history frequencies across sockeye salmon populations in the Wood River basin of southwest Alaska. Using Bayesian hierarchical modelling of fine-scale data from individual spawning populations, I identify habitat characteristics that explain variation in the prevalence of jacks. In Chapter Two, I develop an age-structured population model to investigate the causes of an increase in the prevalence of jacks in a single sockeye salmon population on Kodiak Island Alaska that has developed over the last two decades. Finally, in Chapter Three, I develop an evolutionary-ecological simulation model to explore how stochastic population dynamics affect the maintenance of alternative life histories and evaluate empirical support for this relationship using long-term monitoring data from natural populations throughout North America. In Chapter Three, I also explore interactions between population dynamics, frequency-dependent selection, and size selective harvest, and demonstrate that frequency-dependent mating can filter how populations respond to harvest-induced selection, with important implications for fisheries management.

Chapter 1. ASSOCIATIONS OF STREAM GEOMORPHIC CONDITIONS AND PREVALENCE OF ALTERNATIVE REPRODUCTIVE TACTICS AMONG SOCKEYE SALMON POPULATIONS [1]

1.1 ABSTRACT

In many species, males may exhibit alternative life histories to circumvent the costs of intrasexual competition and female courtship. While the evolution and underlying genetic and physiological mechanisms behind alternative reproductive tactics are well studied, there has been less consideration of the ecological factors that regulate their prevalence. Here, we examine six decades of age composition records from thirty-six populations of sockeye salmon (Oncorhynchus nerka) to quantify associations between spawning habitat characteristics and the prevalence of precocious sneakers known as ‘jacks’. Jack prevalence was independent of neutral genetic structure among stream populations, but varied among habitat types and as a function of continuous geomorphic characteristics. Jacks were more common in streams relative to beaches and rivers, and their prevalence was negatively associated with stream width, depth, elevation, slope and area, but positively related to bank cover. Behavioral observations showed that jacks made greater use of banks, wood, and shallows than guard males, indicating that their

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reproductive success depends on the availability of such refuges. Our results emphasize the role of the physical habitat in shaping reproductive tactic frequencies among populations, likely through local adaptation in response to variable fitness expectations under different geomorphic conditions.

1.2 INTRODUCTION

In species where sexual selection is intense and mating success highly variable, males may adopt alternative reproductive tactics (Gross, 1996, Mank & Avise, 2006). Individuals employing such behaviors often vary from typical males in size and age at maturity (Berejikian et al., 2011, Gross, 1985), morphology (Berejikian et al., 2010), allometry (Flannery et al., 2013), gamete performance (Flannery et al., 2013, Butts et al., 2017) trophic ecology (Johnson & Schindler, 2013), gene expression (Aubin-Horth et al., 2005), and behavior (Foote et al., 1997, Berejikian et al., 2010). While the evolution and proximate genetic and hormonal bases of alternative reproductive tactics have been subject to extensive theoretical and laboratory examination (Mank & Avise, 2006, Maugars & Schmitz, 2008, Gross, 1984), exploration of the ecological mechanisms regulating their occurrence in wild populations is somewhat scarce. Alternative reproductive phenotypes can affect the strength of sexual selection (Jones et al., 2001) and dimorphism (Weir et al., 2016), have economically relevant demographic consequences (Myers, 1984), and implications for the management of commercially valuable populations (Peterman, 1982). As such, it is important to understand the ecological factors that regulate tactic frequencies in the wild.

For many organisms, determining how habitat features influence reproductive tactic frequencies is hindered by uncertainty about the precise spatial distributions occupied during relevant life history stages, such as during breeding and maturation. Anadromous salmonids offer an excellent opportunity to investigate the relationship between physical habitat characteristics and tactic prevalence due to their fine-scale population structure and natal philopatry. Male salmon adopting alternative reproductive tactics typically mature early, returning to spawn after a brief ocean residency (i.e. ‘jacks’ in Pacific Salmon (Oncorhynchus spp.,), and ‘grilse’ in Atlantic salmon (Salmo salaar)), or entirely forgoing marine migration altogether (i.e. sexually mature parr in Atlantic and Chinook salmon (O. tshawytscha) (Johnson et al., 2012, Fleming, 1996). Such precocious males exhibit small body size and subtle secondary sexual characteristics compared to their older counterparts (often referred to as ‘hooknose’ males), relegating them to a reproductive tactic that relies on sneaking rather than direct intrasexual competition and female courtship (Gross, 1985, Healey & Prince, 1998), although they may exhibit such behaviors in the absence of larger competitors (Allen et al., 2007). While either reproductive tactic (sneaking or fighting) is available to both jacks and hooknoses, the former are unsuccessful at fighting in the presence of larger males, which are almost always present in wild populations, and the latter are largely unable to utilize refuges and sneak effectively (Gross, 1985, Gross, 1991b). Consequently, jacks and hooknoses achieve the vast majority of their matings through sneaking and fighting respectively, such that maturation and reproductive phenotypes are effectively conflated in practice (Gross, 1984, Gross, 1991b). Indeed, situations conducive to sneaking will generally favor the reproductive success of jacks, and select for early maturation as well.

Alternative maturation phenotypes in salmonids are generally thought to be the result of a conditional strategy in which individuals may assume different life history pathways depending on their physiological status (Aubin Horth & Dodson, 2004, Gross, 1985). For an individual to mature early, it must achieve a genetically determined population/habitat-specific condition threshold by a particular point in its life cycle (Aubin Horth & Dodson, 2004, Piché et al., 2008). Despite their smaller adult size, juveniles that ultimately mature early are the fastest growing and largest at age of their cohort (Berejikian et al., 2011, Hutchings & Jones, 1998). An individual's ability to acquire resources and efficiently convert them into growth or lipid storage determines whether or not it will achieve the threshold condition necessary for early maturation (Shearer & Swanson, 2000, Shearer et al., 2006). There is evidence for genetic determination of growth rate and juvenile size among salmonids (Garant et al., 2003, Garant et al., 2002, Aubin Horth & Dodson, 2004, Berejikian et al., 2011), establishing a probable basis for the observed heritability of age at maturity and reproductive tactic (Heath et al., 2002, Hankin et al., 1993).

In Pacific salmon, the potential fitness advantage of adopting the jack life history is essentially a balance between the relative improvement in survivorship due to factors such as curtailed marine residency (Mathews, 1968) and reduced vulnerability to fisheries (Kendall et al., 2009) and terrestrial predators (e.g. brown bears, *Ursus arctos*) (Carlson et al., 2004), versus the decline in reproductive success incurred by sneaking rather than competing aggressively for direct access to females (Berejikian et al., 2010). Therefore, the larger the survival differential between jacks and hooknose males, the greater the fitness advantage should be to the former (Gross, 1985, Gross, 1991b). Improved reproductive opportunities for sneaking in a given habitat should also increase the potential fitness advantage of adopting the jack life history (Gross, 1991b, Gross, 1985). Importantly, the reproductive success of both jacks and hooknose males is negatively frequency dependent, ostensibly due to intensified competition among jacks for sneaking refuges, and among hooknoses for courtship opportunities (Berejikian et al., 2010, Gross, 1985). At equilibrium, the relative abundance of jacks is expected to be such that their average fitness within the population is roughly equal to that of hooknoses, with each population’s equilibrium jack proportion existing as a function of the unique patterns of mortality and reproductive opportunities experienced by its members (Gross, 1984, Gross, 1991b, Gross, 1985).

In this study, we quantified variation in the prevalence of jacks among spawning populations of sockeye salmon (O. nerka, Walbaum 1792) in the Wood River basin of southwest Alaska. Juvenile sockeye salmon inhabiting these watersheds move from their natal streams shortly after emergence to lacustrine rearing habitats before migrating to the ocean. Consequently, unlike stream-rearing salmonids (e.g. Chinook, coho), sockeye occupy discrete watershed components during rearing and reproduction, allowing the influence of spawning site characteristics on the prevalence of jacks to be examined independently. While within-population associations between local conditions and sneaker prevalence have been observed in other taxa (Gross, 1991a), data of sufficient temporal and spatial scope to reliably estimate the relative abundance of sneakers over multiple populations is uncommon for most organisms (but see (Healey et al., 2000, Young, 1999, Quinn et al., 2001b, Schütz & Taborsky, 2000, Schütz et al., 2010)). Moreover, in salmonids, environmental factors influencing juvenile growth and condition can produce transient fluctuations in rates of precocity (Gross, 1991b, Koseki & Fleming, 2007, Koseki & Fleming, 2006), necessitating long term data on jack proportions to generate reliable estimates for a population. Here, using six decades of age composition data collected across thirty-six sockeye salmon populations, we apply a Bayesian hierarchical approach to characterize variability in jack proportions among populations, and relate this variability to physical spawning habitat characteristics. While previous work in this watershed has demonstrated a relationship between stream characteristics and age at maturity for older males, significant habitat associations with jack prevalence were not detected (Quinn et al., 2001b).

1.3 METHODS

1.3.1 Study Area

The Wood River basin (59°20'N, 148°40'W) consists of a series of five interconnected lakes that drain into Bristol Bay (Fig. 1.1). The region is relatively free from anthropogenic impacts such as barriers to fish passage or hatchery propagation, the latter being particularly important for this analysis as certain hatchery practices have been shown to increase the relative abundance of jacks (Hankin et al., 2009, Unwin & Glova, 1997). Salmon in the Wood River system spawn in lake beaches, large rivers, or streams, with genetic (Larson et al., 2014, McGlauflin et al., 2011), morphological (Quinn et al., 2001b), and ecological (Quinn et al., 2001b, Blair et al., 1993, Schindler et al., 2010, Johnson & Schindler, 2013, Lisi et al., 2013) differences between these reproductive ecotypes.

1.3.2 Data Collection

Since the 1950s, the University of Washington's Alaska Salmon Program (ASP) has conducted annual censuses throughout the spawning habitats of the Wood River basin. On streams, surveys are typically conducted during peak spawning by personnel walking upstream and visually counting the number of live and dead sockeye salmon of each sex. After reaching the end of viable spawning habitat or a pre-established end point, otoliths are collected from up to 110 haphazardly chosen carcasses of each sex on the journey downstream. In years when limited spawner abundance precludes this volume of sampling, otoliths are collected from all dead fish present. Jacks have been shown to exhibit similar stream arrival timing and reproductive lifespan to older males, suggesting that survey timing should not bias the sample composition for or against their inclusion (Carlson et al., 2004). On rivers and beaches, otoliths are sampled from carcasses found in shallow water, on banks or sand/gravel bars.

After collection, otoliths are cleaned in soapy water, air-dried, and then examined under a dissecting microscope to determine the number of years spent in freshwater and the ocean (Flain & Glova, 1988). The consistency of otolith sampling has been historically variable across locations and years due to the logistical difficulty of accessing some of the study sites, so we established a minimum threshold of 200 total fish sampled from at least five years of surveys for a site to be included in our analysis. The majority of sockeye salmon spawning in the Wood River system spend 1-2 years rearing in lakes, and an additional 1-3 years in the ocean. Jacks were identified from their otoliths as fish with a marine age of one year (Quinn, 2005, Flain & Glova, 1988). Most jacks (~ 92%) in the Wood River system spend only one year in freshwater as well, although no distinction in freshwater age was made in our analyses. Because otolith collection samples a population's age composition during spawning, our analyses are based on jack proportions calculated by return year. Sufficient continuous, overlapping, sex-specific abundance and age composition data to reconstruct jack proportions by cohort (brood year) were limited, but followed a similar pattern as the return year data (Appendix A, Fig. A1, Table A1).

We used geomorphology data for lotic sites in the Wood River basin to investigate potential associations with habitat characteristics and relative jack abundance. Watershed-scale variables, including slope, elevation, and drainage area were measured using ArcGIS (v10.0, Environmental Systems Research Institute, Redlands, CA, USA) by (Lisi et al., 2013). In-stream geomorphic characteristics, such as bank-full width, glide/riffle depth, and average bank cover width were measured using the method of (Pess et al., 2014).

We also explored evidence for variation in jack prevalence among populations emerging as an artifact of neutral population structure (e.g. founder effects). For instance, if an ancestral population that had evolved a particular jack prevalence colonized a number of streams geomorphically similar to its natal habitat, one might detect a spurious correlation between population jack proportions and geomorphology as a result. To test this alternative hypothesis, the jack prevalence of thirteen Wood River streams was compared to their genetic structure based on previously published data for 90 putatively neutral single nucleotide polymorphisms (SNPs) (Larson et al., 2014, Dann et al., 2012). A complete description of the tissue sampling, DNA extraction, and genotyping protocol for these SNPs can be found in (Larson et al., 2014).

To examine if certain habitat features were used by jacks during spawning attempts that may affect their reproductive success in a given location, we performed an observational study comparing habitat use by jack and hooknose males during spawning. Observations were performed at three separate streams (Lynx, Fenno, and Hidden). At each stream, reaches were identified in which females were actively exhibiting spawning or pre-spawning behaviors, and both jacks and hooknoses were present. In such reaches, two observers would simultaneously observe and record the behaviors of one jack and one hooknose for a period of ten minutes, with behavior and occupancy of in-stream habitat features recorded every fifteen seconds. Behaviors were classified as either approaching females, holding, escaping aggression, pairing alongside a female, or repelling another fish. Habitat features were classified as either open pools or riffles, woody debris, banks, or shallows. Across all three streams, a total of 19 distinct spawning interactions were observed, generating behavioral data on 19 jacks and 19 hooknose males.

Additionally, we measured carcasses (mid-eye to hypural plate) of recently senescent jacks to determine if there was variation in body length among populations, and if this variation corresponded with previously described differences in size at age of hooknose males (Quinn et al., 2001b).

1.3.3 Analysis

Due to the presence of strong (> 0.5) correlations between many of the habitat characteristics measured, a principal component analysis (PCA) (Pearson, 1901) was performed on habitat variables to generate two orthogonal geomorphology axes (referred to as PC1 and PC2). Jack prevalence was modeled using a Bayesian hierarchical framework, which facilitates sharing information between data rich and data poor situations (Link & Sauer, 2002). Under a hierarchical model structure, parameters are estimated simultaneously using all available data, with lower level parameters (e.g. proportion of jacks in location j) considered as random variables drawn from the distributions of higher level parameters (e.g. proportion of jacks across all locations) (Gelman & Hill, 2006). In all models, the observed number of jacks ($J_{i,j}$) at a particular location (j) in a given year (i) was considered to be binomially distributed, with a number of trials equal to the total number of males from which otoliths were collected during a particular sampling event ($N_{i,j}$), and some probability of observing a jack ($p_{i,j}$).

$$J_{i,j} \sim B(p_{i,j}, N_{i,j}) \tag{1.1}$$

Due to the presence of overdispersion and lack of fit, specifically with regard to the frequency of zeroes counted (Fig. 1.2), extra-binomial variance in the probability of observing a jack (p) was allowed through a conjugate beta prior distribution on the binomial likelihood, which improved model fit.

$$p_{i,j} \sim Beta(a_{i,j}, b_{i,j})\ ) \tag{1.2}$$

The shape parameters of the beta distribution (a and b) were parameterized in terms of its mean (μ) and concentration (κ).

$$a_{i,j} = (\mu_{i,j})\kappa) \tag{1.3}$$

$$b_{i,j} = (1\text{-}\ \mu_{i,j})\kappa) \tag{1.4}$$

To prevent posterior draws outside the possible range of 0 to 1 for μ, this parameter was logit-transformed and then modeled as a linear combination of spawning location (L_j) and year (Y_i), each of which was drawn from a hyperdistribution with its own mean (μ_L, μ_Y) and standard deviation (σ_L, σ_Y).

$$\text{Logit}(\mu_{i,j}) = L_j + Y_i) \tag{1.5}$$

$$Y_i \sim N(\mu_Y, \sigma_Y)\ ) \tag{1.6}$$

Relative jack abundance associated with a given location (L_j) was described through a suite of different model structures specifying μ_L, the first of which was based on the habitat type to which that site belonged (H_n, where *n* = beach, river or stream).

Model 1: $L_j \sim N(H_n, \sigma_L)$

We also considered a model in which μ_L was based on a population's rearing lake (R_k, where k = Aleknagik, Nerka, Little Togiak, Beverley, or Kulik).

Model 2: $L_j \sim N(R_k, \sigma_L)$

Additionally, we fit a model in which locations were drawn from a common distribution, irrespective of habitat type.

Model 3: $L_j \sim N(\mu_L, \sigma_L)$

Last, we also considered a model structure in which variation among populations was ignored, and jack proportion was solely a function of year.

Model 4: $L_j = 0$

Among lotic habitats for which geomorphology data was collected (23 streams and one river), we fit a model in which location effects were linear functions of geomorphology PCA axes.

Model 5: $L_j \sim N(\mu_L, \sigma_L)$

Where: $\mu_L = \alpha + \beta_1 PC1_j + \beta_2 PC2_j$

Additionally, we considered an alternative formulation of model 5 in which the intercept term (α) was specific to a population's rearing lake (α_k, where k = Aleknagik, Nerka, Little Togiak, or Beverley, as geomorphology data were not available for any Kulik Lake populations).

Model 6: $L_j \sim N(\mu_L, \sigma_L)$

Where: $\mu_L = \alpha_k + PC1_j + \beta_2 PC2_j$

Hyperpriors for σ_L, and σ_Y were drawn from broad uniform distributions from 0 to 1000. R_k, H_n, α, β, and μ_L(unless otherwise specified) were drawn from normal distributions with a mean of 0 and standard deviation of 10^6, and μ_Y was fixed at 0. The concentration parameter (κ) was drawn from a uniform distribution from 1 to 100, as the parameterization of the beta distribution used does not allow values less than one for this term (Kruschke, 2014). Alternative ranges for these priors were attempted, and did not substantially alter model outcomes. Posterior distributions were sampled using Markov chain Monte Carlo (MCMC) routines executed by Just Another Gibbs Sampler (JAGS) (Plummer, 2003) version 4.2.0 implemented in R (R Development Core Team 2015) using the 'rjags' (Plummer, 2013), 'R2jags' (Su & Yajima, 2012), and 'runjags' (Denwood, 2016) packages. Convergence was assessed via the Gelman-Rubin diagnostic (Gelman & Rubin, 1992), which was less than 1.01 for all parameters. Additionally, trace plots and correlograms of each chain for each parameter were examined to assess autocorrelation. Goodness of fit was assessed by plotting the predictive distribution relative to the observed data (posterior predictive check), model performance was validated using simulated data, and where applicable, model selection was performed using the Widely Applicable Information Criterion (WAIC) assuming a binomial error structure. WAIC is well suited for evaluating the predictive accuracy of Bayesian models (Watanabe, 2010), and is applicable to hierarchical designs (Hooten & Hobbs, 2015).

To test whether similarity in jack proportions among populations corresponded with genetic differentiation, we compared pairwise F_{st} values among thirteen stream populations to pairwise differences in median posterior estimates for their jack prevalence using Mantel's test with 100,000 randomizations. Additionally, we plotted symbols scaled chromatically by median posterior estimates for each population's jack prevalence over a neighbor-joining tree based on Nei's DA distance for 90 neutral SNPs (Larson et al., 2016b, Dann et al., 2012). Genetic structure in the Wood River basin is relatively shallow and largely driven by adaptive differences between reproductive ecotypes (Larson et al., 2014, Larson et al., 2016a, McGlauflin et al., 2011). As such, only stream populations were included in this analysis to avoid spurious correlations due to variation in genetic structure and jack prevalence among ecotypes.

To examine interactions between habitat use, behavior, and phenotype, we analyzed the counts from our behavioral observations using a four-way contingency table and nested log-linear models assuming Poisson-distributed error. Alternative models were compared, with the significance of particular levels of interaction assessed using χ^2 tests of deviance.

With jack proportions estimated from otolith samples, it is possible that variation among populations could emerge through habitat-mediated variability in size-selective carcass recovery (Zhou, 2002). To assess any such sampling bias, we compared mean population jack proportions calculated from otolith samples to averages based on visual surveys of live individuals. Within the past 10 years, ASP researchers have distinguished jacks from hooknose males in surveys of live spawning fish in the majority of streams, generating population-specific estimates of jack prevalence that are not subject to potential biases in carcass recovery. Mean jack proportions calculated from otolith samples were regressed against averages derived from live surveys, and the residuals of this regression were in turn regressed against geomorphology axes to assess if sampling bias varied as a function of habitat characteristics.

1.4 RESULTS

For all 36 sites considered, there was similar support for structuring populations by habitat type (model 1, ΔWAIC = 0.39, rearing lake (model 2, ΔWAIC = 0), or within a single common distribution (model 3, ΔWAIC = 0.48). However, there was little support for model 4 (ΔWAIC = 8.41), in which only interannual variation was considered, and site-level effects on jack prevalence were ignored. The effects of spawning habitat type and rearing lake were confounded since each lake differs substantially in its composition of habitat types (Figs 1-2). However, structuring location effects by their habitat type reduced the residual error term (σ_L) while structuring locations by rearing lake did not, despite the additional number of fixed effects (5 lakes versus 3 habitat types) (Fig. 1.3). Median posterior estimates of jack proportions in stream, beach and river spawning populations were approximately 0.006, 0.004, and 0.002 respectively (Fig. 1.3).

Axes one and two of the principal component analysis explained the majority of variability in stream geomorphic characteristics considered, accounting for 44% and 33% of the total variance respectively. Bank-full width, riffle depth, glide depth, and drainage area loaded positively onto the first axis, while the second axis described an increasing gradient of watershed slope and elevation, and decreasing bank cover width (Fig. 1.4). Jack prevalence was negatively associated with PC axis 1 ($\beta_1$median = -0.236; 95% credible interval = -0.380 to -0.090) and positively associated with PC axis 2 ($\beta_2$median = 0.195, 95% credible interval = 0.026 to 0.367). These results suggest that small, shallow, flat, low elevation streams with substantial bank cover favor greater jack prevalence (Fig. 1.4). Inclusion of geomorphology axes reduced the location-level error term (σ_L) by approximately 32% (Fig. 1.5). The addition of lake-specific intercept terms (model 6) failed to substantially improve model fit from the single intercept structure (model 5) (ΔWAIC = 0.71) or explain any additional residual variance in jack prevalence among locations (Fig. 1.5). Moreover, with the exception of Little Togiak, median lake effects in model 6 were generally similar to one another (Fig. 1.5). There was a strong, significant relationship between jack proportions calculated from otolith samples and those based on live censuses, with very little of the deviation between these estimates explained by geomorphology (Appendix A, Fig. A2).

There was no significant difference in associations with habitat features and behaviors between jacks and hooknose males across the three streams at which observations were made. (Lynx, Fenno, Hidden) (χ^2_{32}= -0.088, p > 0.99). However, interactions between stream, phenotype, and behaviors (χ^2_{40}= -58.125, p < 0.001) and stream, phenotype, and habitat features (χ^2_{40} = -44.229, p < 0.001) were each significant. These results indicate that jacks and hooknoses differ in both habitat use and behavior, and that the nature of these differences varies across streams. The relative distribution of habitat occupancy and behaviors among phenotypes indicates that jacks made comparatively greater use of refuges such as undercut banks, woody debris, and shallow areas, primarily to hold, escape aggression, or approach females (Fig. 1.6). Among sites, jacks exhibited greater use of pools, banks and woody debris in Lynx creek, equal use of both shallows and woody debris in Hidden creek, and relatively greater use of shallow areas at Fenno Creek (Fig. 1.6). Conversely, hooknose males made little use of structural features, spending most of their time in open pools or riffles approaching or actively courting females (Fig. 1.6).

There was no statistical support for an association between neutral genetic differentiation and similarity in estimated jack prevalence (Mantel R = 0.3, $p \geq 0.08$). Within each basin, some genetically proximate streams also exhibited similar estimates of jack prevalence, although this was not always the case (e.g. Teal Creek, Fig. 1.7).

Body lengths of jacks were somewhat variable, but uncorrelated with variation in the lengths of older fish across populations (Fig. 1.8). Correlations between the average lengths of jacks and ocean age two (Pearson's ρ = 0.07, t_{19} = 0.31, $p \geq 0.75$) and three (Pearson's ρ = -0.02, t_{19} = -0.11, $p \geq 0.90$) fish were not significant. In contrast, the average lengths of older age classes were significantly correlated across populations (Pearson's ρ = 0.51, t_{19} = 2.62, p <

0.05). A population's average percentage of males with a marine residency of three years is positively related to stream width (Quinn et al., 2001b), and both of these variables were negatively correlated with jack prevalence (Fig. 1.9).

1.5 DISCUSSION

Our results demonstrate that jack prevalence varies consistently among stream populations of sockeye salmon as a function of geomorphology, with some limited support for differences among discrete spawning habitat types (i.e. reproductive ecotypes) as well. There was no evidence of geomorphically-based sampling bias, suggesting that habitat-mediated intrasexual and natural selection regimes regulating the fitness of jacks likely contribute to the observed variability among stream populations. It is difficult to disentangle the effects of rearing lake from habitat type since the majority of streams are found in lakes Aleknagik and Nerka, the majority of beaches are found in lake Beverley, and Little Togiak and Kulik lakes are each represented by only a small number of populations each. However, inclusion of lake effects failed to explain additional variation in jack prevalence among populations at the system-wide scale (Fig. 1.3), or among lotic populations only (Fig. 1.5). Nonetheless, because live count data were not available for beach or river populations, we cannot rule out sampling bias as a possible explanation for the observed differences between habitat types, and recommend these results be interpreted cautiously.

In a review of data on the reproductive success of sneaking by smaller males among salmonids, Hutchings and Myers (1988) concluded that its effectiveness is negatively related to the size differential between males, presumably a function of the positive relationship between gonad size, sperm volume, and body size (Foote et al., 1997, Moller, 1991). While we observed variation in the lengths of jacks across populations, this variability was not coherent with variation in the length-at-age of older males, suggesting that the size differential between phenotypes may be reduced in populations with smaller hooknose males. It is possible that variation in the size of jacks does not track that of their older counterparts because the decision to adopt the jack life history is made in freshwater (Vøllestad et al., 2004). If so, jacks would accumulate the majority of their body mass at sea after having already reached the threshold to mature after their first ocean year, decoupling marine growth from the maturation decision. Moreover, jacks may not experience the same habitat-mediated selection on body size as older males if they are not subject to substantial bear predation (Quinn & Kinnison, 1999, Ruggerone et al., 2000, Carlson et al., 2004) or limited spawning site accessibility (Quinn et al., 2001b, Ramstad et al., 2010) across the full range of potential body sizes for marine age one fish.

Previous morphometric analyses on sockeye salmon have shown that adult body size is largest in beach spawners, followed by river and then stream fish (Quinn et al., 2001b). Among lotic habitats (rivers and streams), both size at age, and duration of marine residency are positively related to channel width and depth (Quinn et al., 2001b), with individuals spending three years in the ocean reaching substantially larger body sizes than marine age two fish. Consequently, stream spawning jacks, particularly those occupying shallow, narrow habitats, may enjoy better reproductive success due to their greater relative size among males in the population. Direct comparison between jack prevalence and the average size differential between jacks and older fish among populations indicated a weak, negative relationship (Appendix A Fig. A3). It should also be noted that the negative association of jack prevalence with stream width and depth is consistent with patterns in the age composition of hooknose males (Quinn et al., 2001b), and may simply be an extension of a general relationship between these habitat characteristics and salmon age at maturity.

Morphological variation in salmon across habitats is strongly associated with variability in bear predation pressure, which is constrained by geomorphology as well (Quinn et al., 2001b). Bear predation on salmon is thought to be minimal in beaches and large rivers, and is negatively related to channel depth and width in streams (Quinn et al., 2001b). Given that jacks are less vulnerable to bears due to their reduced body size (Ruggerone et al., 2000, Quinn et al., 2001a, Quinn & Kinnison, 1999, Carlson et al., 2004), the relative survivorship advantage of the jack life history in shallow, narrow streams where predation risk is high is likely greater than in larger streams, beaches or rivers. A greater survivorship advantage should elevate the fitness of jacks relative to typical males, increasing the proportion at which their mean fitness remains equal to that of their older counterparts (Gross, 1985, Gross, 1984, Gross, 1991b).

According to published anecdotal descriptions of spawning events, jacks typically occupy satellite positions downstream of a spawning pair, taking refuge under banks, in shallow areas, side channel pools, or near tree limbs or other debris before rapidly approaching to spawn on the opposite, free side of the female at the onset of oviposition (Carlson et al., 2004, Berejikian et al., 2010, Foote et al., 1997, Gross, 1985). As such, availability of sneaking refuges is likely important to the reproductive success of jacks. Our results indicate greater jack prevalence in small, shallow streams of low elevation and slope with substantial bank cover. Undercut banks tend to occur in low gradient watersheds where riparian vegetation stabilizes the soil such that the surface of the bank remains intact despite erosion at the base. The observation that jacks are more common in locations with substantial bank cover is consistent with theoretical expectations that habitats containing ample sneaking refuges should support populations with greater jack prevalence (Gross, 1991b, Gross, 1985, Gross, 1984). Use of undercut banks for sneaking by jacks has been described previously (Carlson et al., 2004), and our own behavioral study shows that jacks are more likely to use banks than hooknose males, particularly for holding and approaching females. Low gradient streams also exhibit greater concentrations of dissolved organic carbon (Jankowski et al., 2014), decreasing water transparency and potentially facilitating surreptitious spawning advances by jacks (Gross, 1991b). Additionally, use of shallow areas as sneaking refuges (Gross, 1985, Gross, 1991b, Berejikian et al., 2010) may improve reproductive opportunities for jacks in streams with shallow spawning habitats (glides and riffles), potentially contributing to the negative association between jack prevalence and PC1.

The observed variation in jack proportions among populations could be partially attributable to the size selectivity of the Bristol Bay gillnet fishery. Assuming that jacks comprise a negligible portion of catches due to their reduced body size (Kendall & Quinn, 2012, Kendall et al., 2009), variable exploitation rates of older males across populations may differentially skew proportions of jacks in the escapement. For instance, fishing pressure for Bristol Bay sockeye salmon has been shown to disproportionately affect populations composed of larger-bodied individuals (Kendall & Quinn, 2012, Kendall & Quinn, 2009, Kendall et al., 2009) such that jacks, likely experiencing equally negligible fishing mortality across populations, may comprise a greater portion of the escapement in such populations as a result. However, adjusting the recorded jack proportions by exploitation estimates of two and three-year old fish calculated for five populations from 1963 to 2007 by Kendall and Quinn (2009) did not alter the rank-order of model-predicted jack proportions among these populations (Appendix A Fig. A4). As such, we have no evidence to suggest that the observed variation among populations in jack prevalence is an artifact of fishery selectivity.

There was no significant association between genetic similarity and jack prevalence among stream populations, suggesting that the observed habitat associations did not merely arise as an artifact of neutral population structure (e.g. founder effects). Moreover, genetic structure in the Wood River system is shallow, with an overall Fst of ~ 0.01, and no significant differentiation between any population pair presented in Fig. 1.7 (Larson et al., 2014, Larson et al., 2016b). As such, it appears more likely that geomorphic associations with population jack prevalence are the result of adaptive evolution in response to local habitat conditions. Such an explanation is similar to the ‘recurrent evolution’ hypothesis of sockeye salmon life history ecotypes (Wood et al., 2008, Ramstad et al., 2010). Under this model, strays from a loosely differentiated ancestral ecotype colonize available lake habitat between glaciation events, leading to the recurrent parallel evolution of locally adaptive traits among polyphyletic lineages. Similarly, we propose that a population’s proportion of jacks is the result of local adaptation to population-specific habitat conditions regulating the relative fitness of the jack life history. A genetically-based threshold for early maturation is likely the proximate trait on which adaptive evolution operates (Piché et al., 2008, Aubin Horth & Dodson, 2004), such that in populations where the relative fitness of jacks is higher, the maturation threshold is relaxed relative to the population average condition.

Discussions of the evolution and maintenance of alternative reproductive tactics have historically emphasized population-level characteristics, such as variance in reproductive success, and frequency dependence (Shuster & Wade, 2003, Mank & Avise, 2006, Gross, 1996), while analyses of their reproductive viability typically occur at the organismal and cellular scale

(Flannery et al., 2013, Butts et al., 2017, Taborsky, 1998). Our results support assertions that ecological factors also play an important role in the evolution and fitness of alternative reproductive tactics (Taborsky, 2001), likely through local adaptation driven by habitat-mediated section on tactic frequencies. Alternative reproductive phenotypes are thought to invade a population when their fitness at low frequency exceeds the average fblaitness of the ‘primary’ tactic (Shuster & Wade, 2003), persisting in an evolutionarily stable state through frequency dependent selection. Our findings suggest that habitat quality can shape the fitness benefits presented to individuals by adopting a given tactic, and regulate the strength of frequency dependent selection acting within a population. These results lend empirical support to previous theoretical (Gross, 1996, Gross, 1985, Gross, 1984, Gross, 1991b) and empirical (Schütz & Taborsky, 2000) work emphasizing the importance of ecosystem-level characteristics in shaping reproductive tactic frequencies, and underscore the importance of considering ecological influences in models of mating system evolution (Taborsky, 2001).

1.6 FIGURES

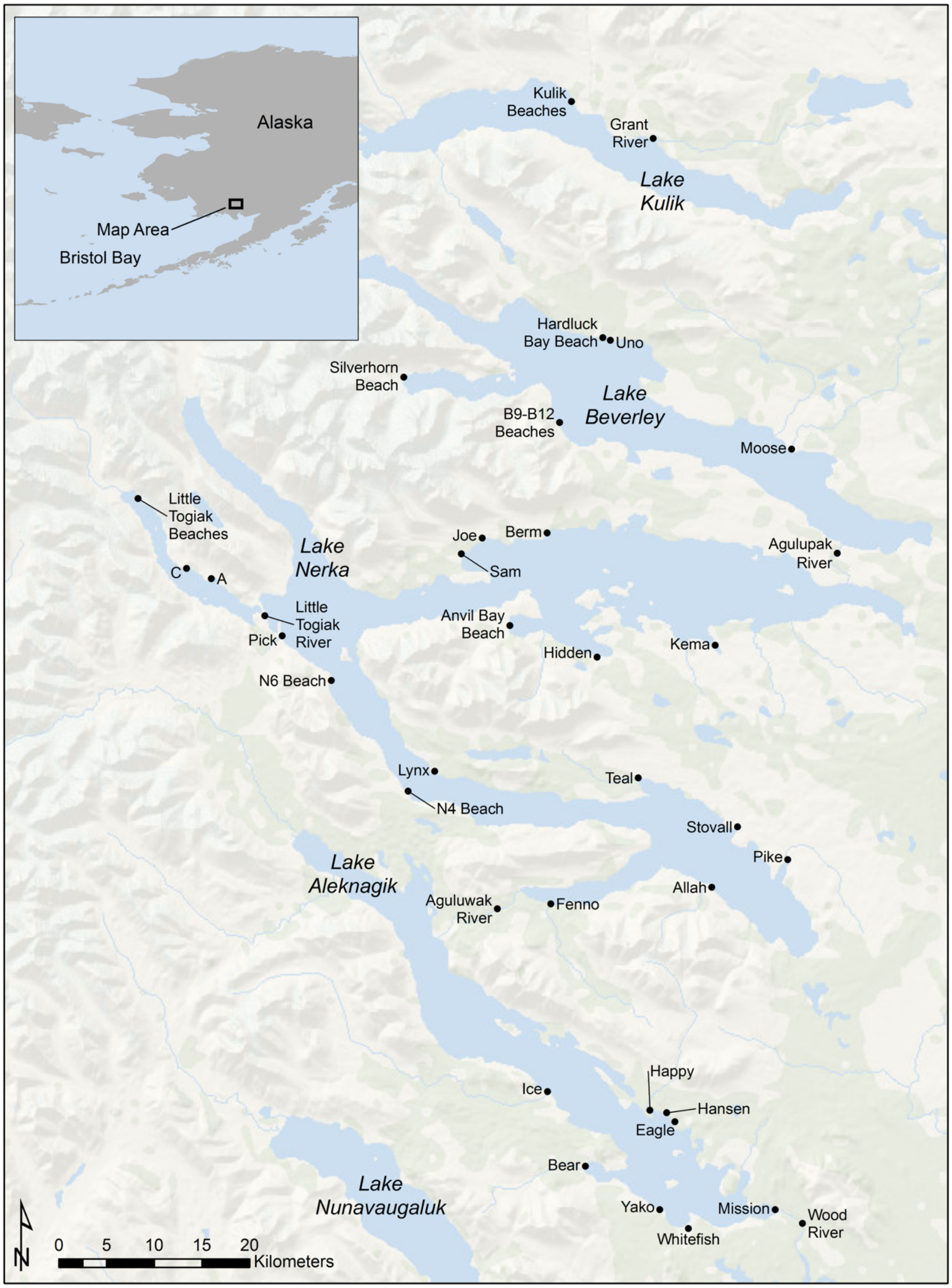

Figure 1.1 Map of the Wood River system and otolith sampling sites.

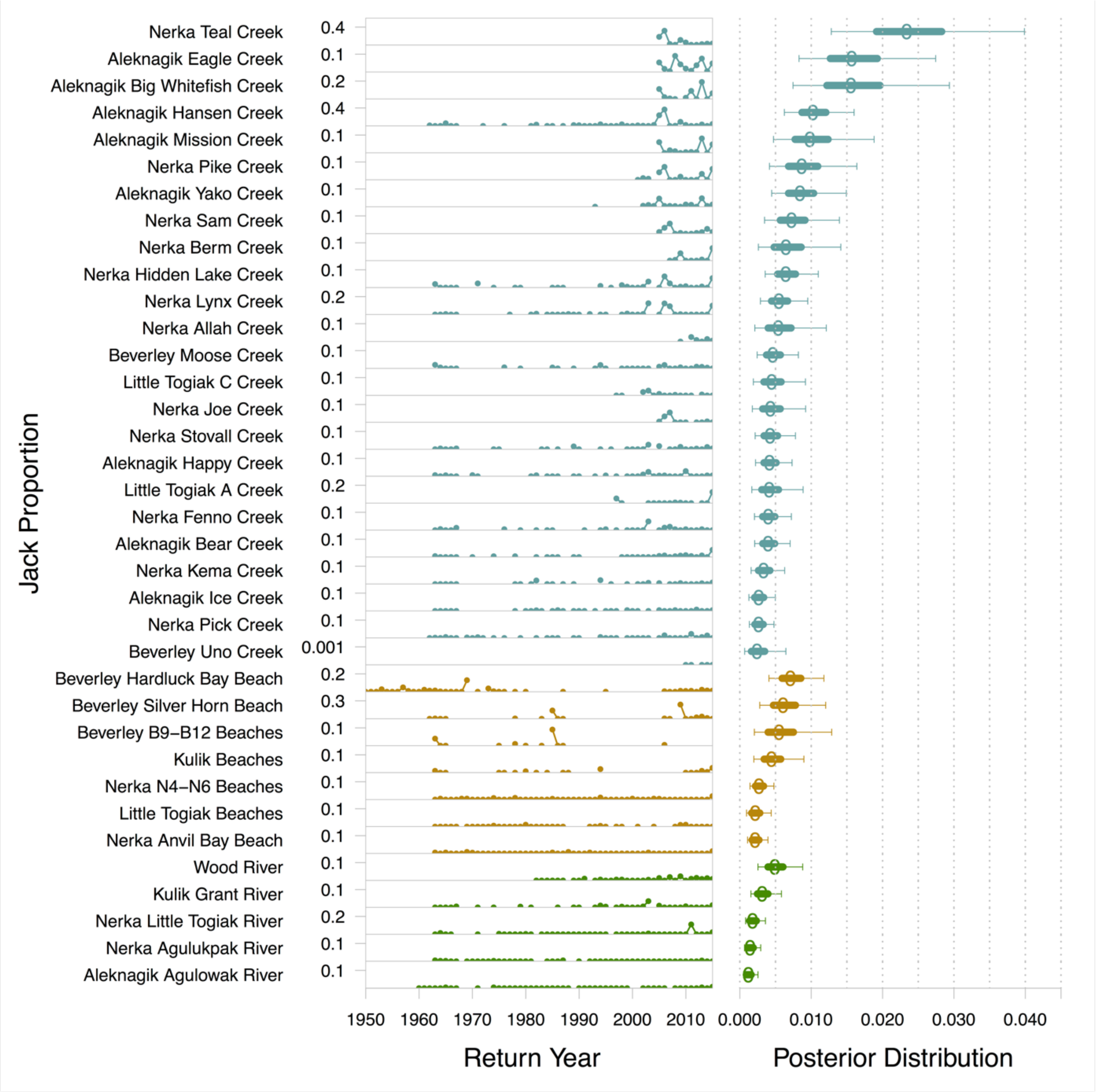

Figure 1.2. Patterns of jack prevalence across spawning populations. Stream populations are pictured in blue, beach populations in brown, and river populations in green. Sparklines depict temporal patterns of observed jack proportions for each population, while adjacent caterpillar plots show the medians (ovals), and 50% (thick lines) and 95% (thin lines) Bayesian credible intervals for each location's jack prevalence.

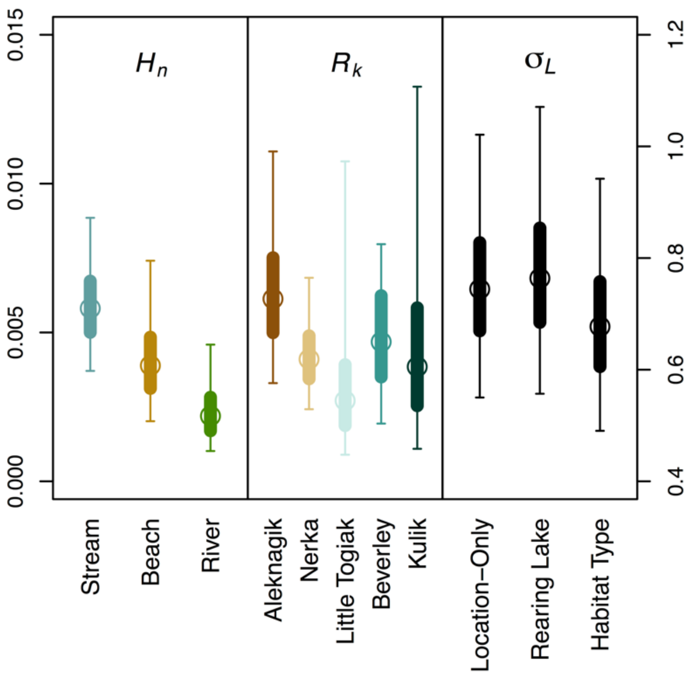

Figure 1.3. Posterior distributions for effects of habitat type (H_n) based on model 1 (panel 1), and rearing lake (R_k) based on model 2 (panel 2) on population jack prevalence. Panel 3 depicts the posterior distribution of σ_L, the standard deviation of the among-location hyperdistribution, under model 1 (habitat type), model 2 (rearing lake), and model 3 (location only). Medians are indicated by circles, and thick and thin lines represent 50% and 95% Bayesian credible intervals respectively. The left axis labels apply to both panel 1 and panel 2.

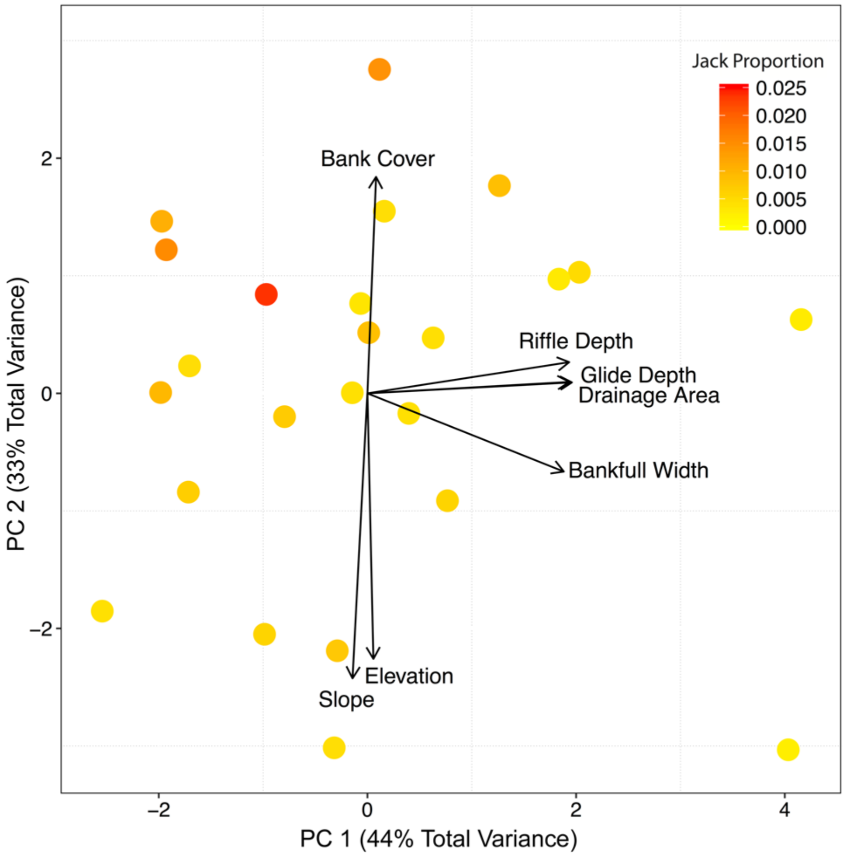

Figure 1.4. Ordination plot of principal component analysis (PCA) of habitat variables for the Wood River system. Characters are scaled chromatically by the posterior median jack prevalence of each population based on an intercept-only version of model 4.

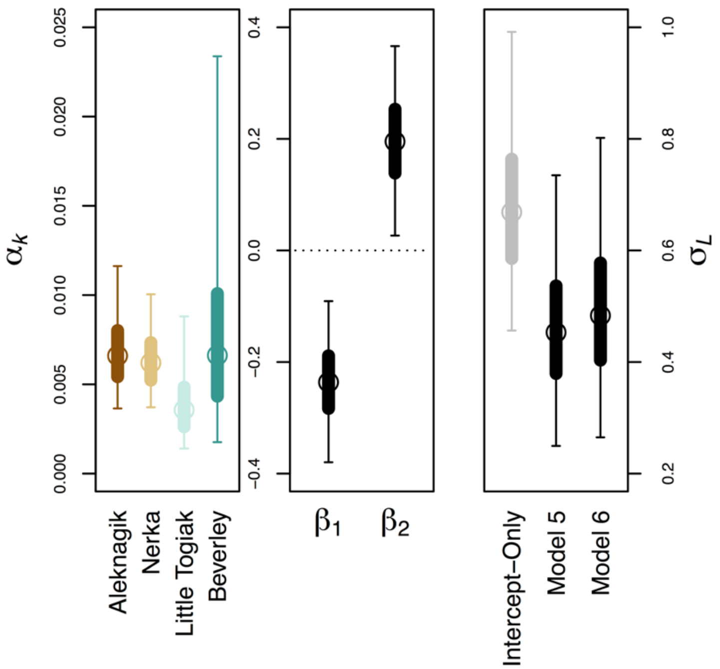

Figure 1.5. Posterior distributions for parameters from models 5 and 6. Panel 1 shows the distributions of lake-specific intercept terms (α_k) from model 6. Panel 2 shows the distributions for the model coefficients for PC1 (β_1) and PC2 (β_2) from model 5, and panel 3 depicts the distribution of σ_L, the standard deviation of the location-level hyperdistribution in models 5 and 6 compared to an intercept-only version without the effects of PC1 and PC2 (grey). Circles indicate medians, thick and thin lines indicate 50% and 95% Bayesian credible intervals respectively.

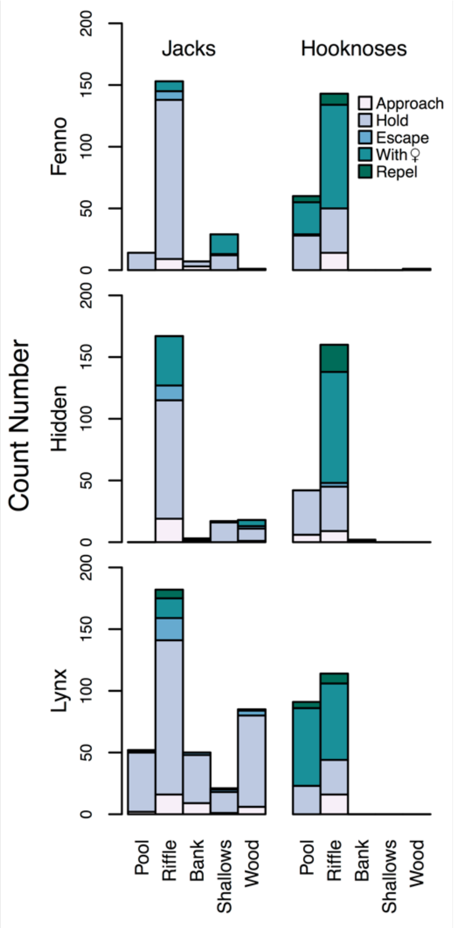

Figure 1.6. Stacked bar plots showing the count frequency with which each phenotype (jacks and hooknose males) were observed using in-stream habitat features at Fenno, Hidden, and Lynx Creeks. Bars are partitioned into the types of behaviors exhibited by individuals within each habitat feature.

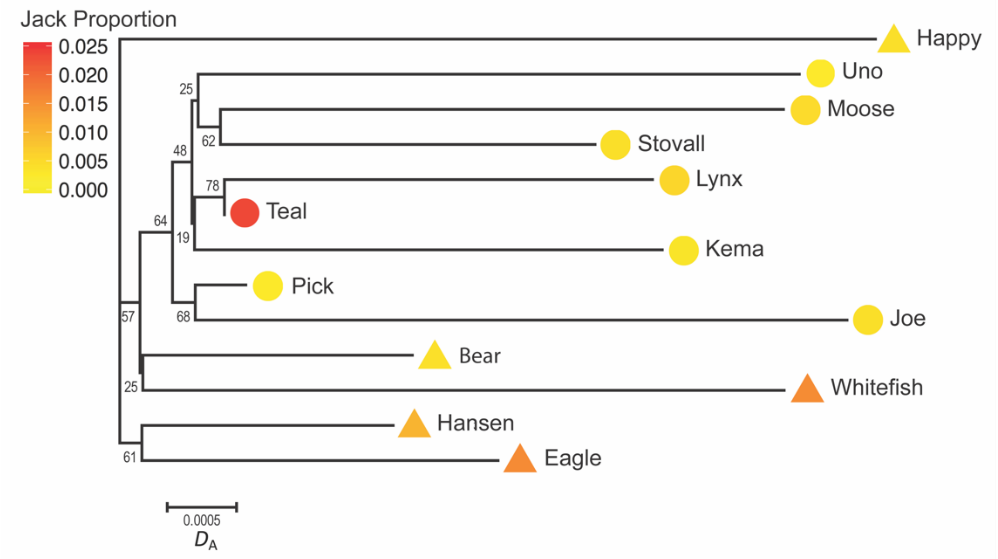

Figure 1.7. Neighbor-joining tree based on Nei's D_A distance for 90 neutral SNPs among Wood River stream population collected by Dann et al. 2012. Symbols are scaled chromatically by the median value of the posterior distribution of each location's jack prevalence. Upper basin (lakes Nerka and Beverley) populations are indicated with circles, while lower basin (lake Aleknagik) populations are indicated by triangles.

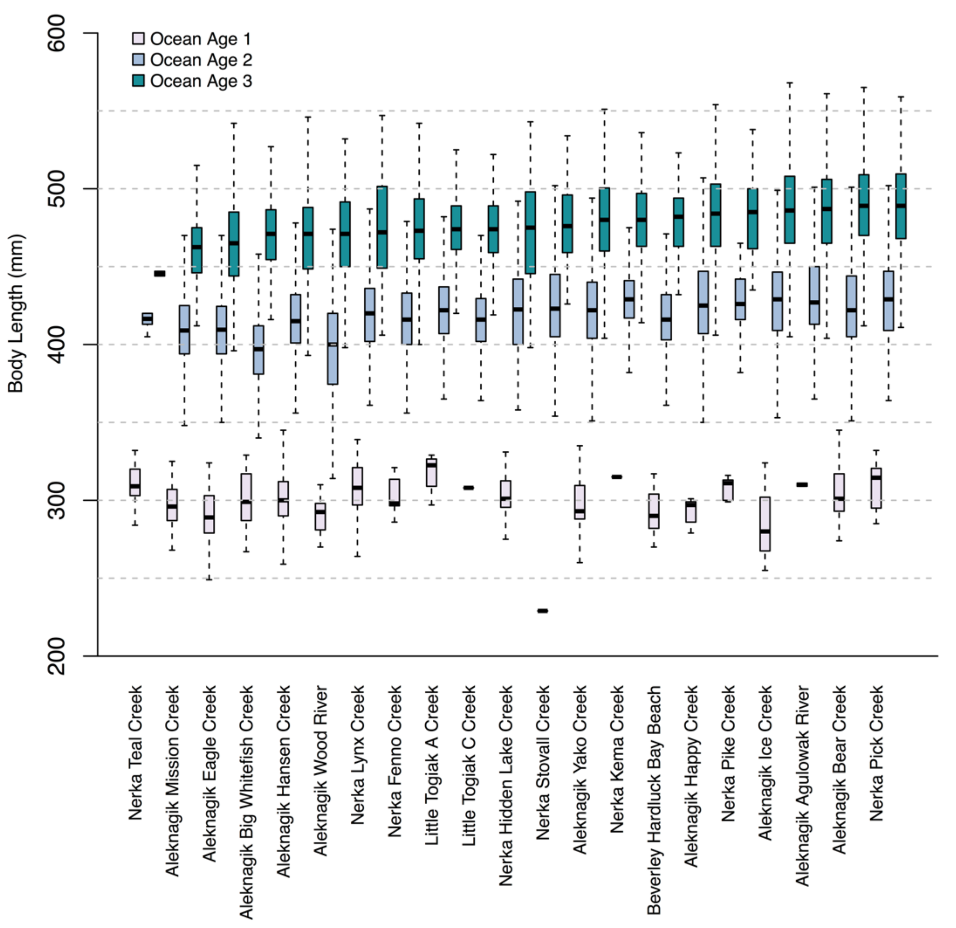

Figure 1.8. Boxplot of length at age for Wood River sockeye salmon populations. Populations are rank ordered by length of ocean age three fish. The smallest and largest observations not considered outliers are represented by the error bars, with the lower and upper quartiles indicated by the upper and lower boundary of the box. The line in the middle of each box indicates the median. Data considered as outliers (not shown) were values beyond 1.5 times the interquartile range.

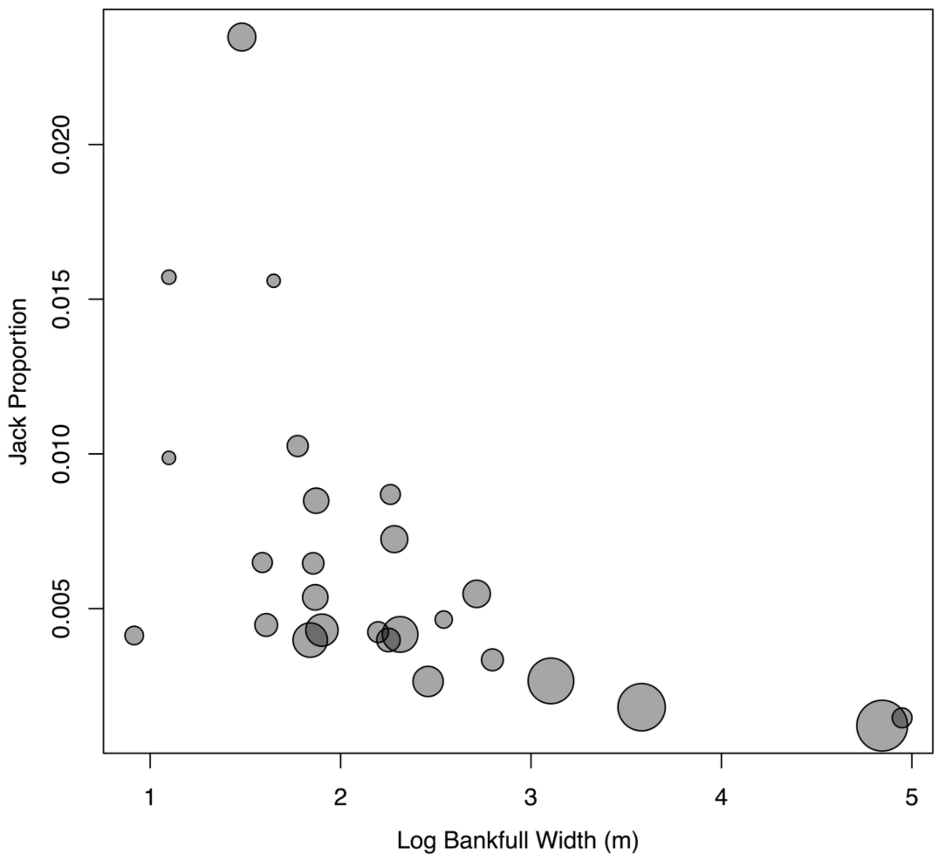

Figure 1.9. Relationship between posterior median jack proportions for lotic habitats based on model 1 and the natural logarithm of bank-full channel width (excluding the Wood River and Grant River for which data was not available). Characters are scaled in size by each population's average percentage of males with a marine age of three years.

Chapter 2. RECRUITMENT VARIATION DISRUPTS THE STABILITY OF ALTERNATIVE LIFE HISTORIES IN AN EXPLOITED SALMON POPULATION [2]

2.1 ABSTRACT:

Males of many fish species exhibit alternative reproductive tactics, which can influence the maturation schedules, fishery productivity, and resilience to harvest of exploited populations. While alternative mating phenotypes can persist in stable equilibria through frequency-dependent selection, shifts in tactic frequencies have been observed, and can have substantial consequences for fisheries. Here, we examine the dynamics of precocious sneaker males called 'jacks' in a population of sockeye salmon (*Oncorhynchus nerka*) from Frazer Lake, Alaska. Jacks, which are of little commercial value due to their small body sizes, have recently been observed at unusually high levels in this stock, degrading the value of regional fisheries. To inform future strategies for managing the prevalence of jacks, we used long-term monitoring data to identify what regulates the frequencies of alternative male phenotypes in the population over time. Expression of the jack life history could not be explained by environmental factors expected to influence juvenile body condition and maturation probability. Instead, we found a strong positive association between the proportion of individuals maturing as jacks within a cohort, and the prevalence of jacks among the males that sired that cohort. Moreover, due to differences in age-at-maturity between male phenotypes, and large interannual variability in recruitment strength, jacks from

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[2] This work has been published:
DeFilippo, L. B., Schindler, D. E., Ohlberger, J., Schaberg, K. L., Foster, M. B., Ruhl, D., & Punt, A. E. (2019). Recruitment variation disrupts the stability of alternative life histories in an exploited salmon population. *Evolutionary applications*, *12*(2), 214-229.

strong year-classes often spawn among older males from the weaker recruitments of earlier cohorts. Through such ‘cohort mismatches’, which are amplified by size-selective harvest on older males, jacks frequently achieve substantial representation in the breeding population, and likely high total fertilizations. The repeated occurrence of these cohort mismatches appears to disrupt the stabilizing influence of frequency-dependent selection, allowing the prevalence of jacks to exceed what might be expected under equilibrium conditions. These results emphasize that the dynamics of alternative life histories can profoundly influence fishery performance, and should be explicitly considered in the management of exploited populations.

2.2 INTRODUCTION

There is increasing awareness that fisheries management must consider the mating systems of exploited taxa to understand the biological consequences of exploitation (reviewed in Rowe & Hutchings, 2003). In fishes, males of the same species commonly exhibit divergent approaches to achieving fertilizations, which can influence the genetic diversity, age and size structure, and fishery productivity of exploited stocks (Jones & Hutchings, 2002; Larsen et al., 2004; Myers, 1984; Rowe & Hutchings, 2003). Reflecting discontinuous variation in one or more traits within a population, the existence of such alternative reproductive tactics (ARTs, *sensu* Taborsky, Oliveira, & Brockmann, 2008) challenged early evolutionary models based on optimization theory, which posit that there is a single ideal life history that should exclude alternatives through natural/sexual selection (Schaffer, 1979; Stearns, 1980). More recently, researchers have adopted a game theoretic view of mating systems in which individual fitness varies based on the activities of others (Maynard Smith, 1982; Oliveira, Taborsky, &

Brockmann, 2008; Shuster & Wade, 2003). In this framework, multiple genetically-based mating tactics can persist in a population when the fitness of each is constrained by frequency-dependent selection (FDS) (Gross, 1984; Shuster & Wade, 2003). By reducing the per-capita reproductive success of a phenotype as it becomes more common, FDS should produce a stable distribution (or stable oscillations, Sinervo & Lively, 1996) of tactics in which alternatives experience equal average fitness (Shuster & Wade, 1991, 2003, but see Tomkins & Hazel, 2007). While the theoretical bases for the stability of ARTs are well-developed (reviewed in Shuster & Wade, 2003; Taborsky et al., 2008) and supported empirically (Berejikian et al., 2010; Bleay, Comendant, & Sinervo, 2007), resolving why certain populations deviate from equilibrium conditions is important for understanding mating system evolution, and the potential consequences of fishery exploitation.

In anadromous Pacific salmon (*Oncorhynchus* spp.), most males compete aggressively on the spawning grounds for mating opportunities after reaching a large body size at sea. In addition to these typical ‘hooknose’ males, males of certain species may also mature as ‘jacks’, which migrate to the ocean but return to freshwater to spawn earlier than the youngest females in the population (Quinn, 2005). Substantially smaller, and with more subtle secondary sexual characteristics than their older counterparts, jacks are generally ineffective at acquiring mates through intrasexual contests and female courtship (Gross, 1984). However, jacks possess numerous morphological and physiological specializations for achieving fertilizations through ‘sneaking’, including a higher gonadosomatic index (Flannery, Butts, Słowińska, Ciereszko, & Pitcher, 2013), improved sperm performance (Young, Conti, & Dean, 2013), and cryptic body coloration compared to older males (Gross, 1984). While either behavior is possible in both male phenotypes (Allen, Rich, & Quinn, 2007; Berejikian, Tezak, & LaRae, 2000), jacks and hooknoses achieve the majority of their matings through sneaking and fighting respectively (Gross, 1984). In order for a juvenile salmon to become a jack, it must reach a critical growth or lipid accumulation threshold by a certain point in its life cycle (Shearer & Swanson, 2000; Thorpe, Mangel, Metcalfe, & Huntingford, 1998). As such, environmental (Koseki & Fleming, 2007; Vøllestad, Peterson, & Quinn, 2004) and genetic (Berejikian, Van Doornik, & Atkins, 2011, but see Hankin, Nicholas, & Downey, 1993; Barson et al., 2015) factors influential to juvenile growth and body condition can contribute to the developmental decision to mature as a jack. Importantly, there are also heritable differences among individuals in the threshold for early maturation (Aubin-Horth, Bourque, Daigle, Hedger, & Dodson, 2006; Baum, Laughton, Armstrong, & Metcalfe, 2004; Piche, Hutchings, & Blanchard, 2008), such that alternative male phenotypes in salmon likely reflect underlying genetic variation in this trait as well (Hankin et al., 1993).

Evidence from theoretical and experimental studies suggests that alternative life histories of male salmon are maintained through FDS, and can experience equal average fitness (Berejikian et al., 2010; Gross, 1984, 1985, 1991; Hutchings & Myers, 1994). In most populations, the percentage of males that mature as jacks remains relatively small over time (DeFilippo et al., 2018), presumably due to the stabilizing effects of FDS. However, some studies have questioned the feasibility of a stable evolutionary equilibrium between alternative male phenotypes in salmon, noting that extrinsic stochastic controls on juvenile growth and survival could preclude such an equilibrium (Koseki & Fleming, 2006, 2007). Moreover, precocious males can become quite prominent in some stocks, degrading fishery performance and posing an intractable challenge to management (Larsen et al., 2004; Zimmerman, Wes Stonecypher, & Hayes, 2003). As such, it is important to understand what regulates the realized dynamics of alternative life histories in salmon to assess how fisheries management decisions may impact their stability.

In a population of sockeye salmon (*O. nerka,* Walbaum, 1792) spawning in Frazer Lake on Kodiak Island, Alaska, jacks have recently been observed at extraordinarily high levels, accounting for over half of spawning males in some years (Foster, 2008). Because they are of little commercial value due to their small body sizes and perceived unmarketability, the elevated prevalence of jacks in Frazer Lake sockeye runs has led to substantial economic losses for local fisheries, and growing uncertainty about the population's future (Jackson & Keyse, 2015). In 2014 and 2015, mounting public concern over the issue led to a cull on jacks by management in an attempt to reduce their levels in the population. The financial and logistical burdens imposed by these efforts, coupled with concerns about potential negative effects on stock productivity and genetic diversity led to a decision in 2016 to discontinue culling (Foster & Schaberg, 2016). Here, we examine the temporal dynamics of jacks in Frazer Lake sockeye salmon to inform future management approaches to mitigating their proliferation. While previous experiments have identified proximate determinants of reproductive life history at the individual level, our approach integrates long-term demographic and environmental data to explore what regulates a population's realized jack prevalence over time. Our results emphasize the importance of genetic factors in expression of the jack life history, and reveal a novel mechanism arising through stochastic population dynamics that may ultimately determine the stability of ARTs in salmon.

2.3 METHODS

2.3.1 Study Site

Located on the southern end of Kodiak Island, Alaska (57°15’ N, 154°10’ W), Frazer Lake drains to the southwest into Olga Bay via Dog Salmon Creek (Fig. 2.1). An impassable waterfall on the upper portion of Dog Salmon Creek originally prevented upstream migration by anadromous salmon to Frazer Lake (Ruhl, 2017). In an effort to create an economically viable salmon run, sockeye adults, eggs and fry were stocked in Frazer Lake from 1951-1971 using broodstock primarily from Red Lake (Ayakulik stock), and also Karluk Lake (Fig. 2.1C) and Ruth Lake/Becharof Lake on the Alaska Peninsula (Fig. 2.1B) (Blackett, 1979; Burger, Scribner, Spearman, Swanton, & Campton, 2000). Adult salmon returning to spawn were initially backpacked over the falls to access the lake until the construction of a fish ladder in 1962, followed by the installation of a second parallel fishway in 1979 (Kyle, Koenings, & Barrett, 1988). Run sizes increased substantially from 1974 to 1985, leading to concomitant declines in zooplankton biomass and juvenile body condition (Kyle et al., 1988). In an attempt to mitigate these density-dependent effects on juvenile growth, nitrogen and phosphorus fertilizers were added to Frazer Lake from 1988 to 1992, leading to significant increases in zooplankton biomass (Kyle, 1994). There have been no further efforts to enhance the habitat quality of Frazer Lake since 1992. Since the development of a self-sustaining run in Frazer Lake, this population has become one of the most commercially valuable stocks in the region. Harvest of Frazer Lake fish occurs within the Alitak district, primarily in a gillnet fishery operating in the Alitak, Moser, and Olga Bay sections, with a lesser degree of purse seine harvest in the Cape Alitak and Humpy-Deadman areas as well (Fig. 2.1C; Foster, 2008).

2.3.2 Data Collection

In exploited salmon stocks, the number of fish that successfully migrate past fisheries and arrive on the spawning grounds in a given year is referred to as the ‘escapement’. The individuals within the escapement comprise that year’s reproductive population, or ‘spawners’, and their offspring that reach maturity are the ‘return’ from that ‘brood year’. Because age-at-maturity is variable within most populations, offspring produced from a given brood year reach maturity and spawn across multiple different calendar or ‘return years’. A ‘run’ refers to a group of fish that share the same return year, which includes individuals produced from multiple brood years. The return year age composition is useful for understanding the contributions of each age class to the harvest and breeding population, while the brood year age composition reflects the maturation schedules of individual cohorts. Data on run size and age composition are collected by return year, and the abundance of each age class is lagged by its total age to calculate numbers-at-age produced from a given brood year in a process known as ‘run reconstruction’. The Alaska Department of Fish and Game (ADF&G) maintains such data for Frazer Lake sockeye salmon with information on cohorts from as early as the 1968 brood year, although the raw abundance and age composition data used to develop the run reconstruction are not available prior to 1986, when more intensive population monitoring began.

Each year, the ADF&G counts and samples adult sockeye salmon returning to spawn in Frazer Lake (described in Ruhl, 2017). Fish are counted as they enter Dog Salmon Creek and again when they pass through the fish ladders, where they are also sexed, and the number of jacks (based on visual identification and length measurements, e.g., Carlson, Rich, & Quinn, 2004) is recorded. The annual age composition of the escapement is determined by visual examination of scales (Gilbert, 1913; Mosher, 1969) taken from samples of adult salmon as they pass through the fish ladders. Frazer Lake sockeye salmon typically spend 1-3 years rearing in the lake, followed by an additional 1-3 years in the ocean, with 2 years being the most common period of lacustrine and marine residency for this population. All fish spend their first year of life overwintering in the gravel, but we do not include this period in our assignment of ‘freshwater age’. In sockeye salmon, ‘hooknose males’ typically mature at ocean age-2 or 3 while jacks are defined as males with a marine residency of 1 year, and were identified as such from the scale samples (ocean age-1 females are very rare (Quinn, 2005)). Some age classes were only marginally represented in the age distribution (ocean age-4/freshwater age-4) and were removed to reduce the number of estimated parameters in our models (see Methods: Analysis). Individuals with freshwater and marine residencies of 1-3 years were retained in our analyses, generating a total of 9 unique age combinations (e.g., ocean age-1, freshwater age-1 etc.) that accounted for ~ 98% of individuals in the population.

The age composition of harvested fish is determined from scale samples taken from commercial landings within the Alitak district (described in Foster, 2008; Moore, 2014). Due to the mixed stock nature of these fisheries, Frazer Lake fish are harvested with sockeye salmon from the Upper Station (South Olga Lakes) population (Fig. 2.1C). Historically, harvested fish were assigned to their population of origin using age-specific scale pattern analysis (SPA, Marshall et al., 1987) until 2001, when the SPA project was discontinued. Since then, the abundance and age composition of harvested Frazer Lake and Upper Station fish have been determined by assuming equal exploitation rates between stocks and inferring the relative contribution of each population to the harvest using the ratio of their escapements. Ratios are calculated as three-day moving averages based on specified travel times between the harvest areas and weirs at which daily escapements for both populations are enumerated (Foster, 2008).

We obtained time-series of several environmental variables to evaluate as covariates when modelling the dynamics of jacks in Frazer Lake sockeye salmon (see Methods: Analysis). Annual Kodiak air temperatures were obtained from the National Weather Service Forecast Office, Fairbanks AK, and annual values of the North Pacific Gyre Oscillation (NPGO, Di Lorenzo et al., 2008) — an index of basin-scale oceanic conditions relevant to salmon productivity — were downloaded from the online repository for these data (http://www.o3d.org/npgo/npgo.php). The average seasonal biomass of the main zooplankton genera comprising the diets of juvenile Frazer Lake sockeye salmon (*Daphnia* and *Bosmina,* Kyle et al., 1988) were estimated each year based on the protocol described in Ruhl (2013). An estimate of zooplankton biomass was not available for the first year in which covariate effects were evaluated, so a value was imputed using the average of the following two years' estimates.

2.3.3 Analysis

Our analysis had three goals; (1) determining if there have been any changes in the proportion of Frazer Lake sockeye salmon maturing as jacks within cohorts over time (by brood year), (2) evaluating which, if any, environmental and demographic variables influence the proportion of individuals maturing as jacks within cohorts, and (3) comparing patterns of variability in the dynamics of the population's main ocean age classes by brood versus return year. For goal 1, we were interested in estimating the general trend in jack proportions over the history of this population, so we fit a simple Bayesian random walk model to values of brood year jack proportions calculated from the ADF&G run reconstruction. While the reconstructed brood year age composition is available for most of the population's history (as far back as brood year 1968), it does not have information on the sampling effort (e.g., scale sample sizes) for these early cohorts that would be necessary to reliably distinguish process from observation error in a state-space framework. To explore finer-scale temporal dynamics in the age composition of the population (goals 2-3), we developed a series of age-structured Bayesian state-space models (e.g. Fleischman, Catalano, Clark, Bernard, & Chen, 2013; Staton, Catalano, & Fleischman, 2017) for the time period in which the raw abundance and scale age composition data were available (return years 1986-2015). The core process components of these models take two general forms; the first quantifies the effects of various environmental and demographic covariates on the production of jacks within cohorts by brood year (goal 2). The second form estimates temporal patterns in the abundance of the population's main ocean age classes by both brood and return year (goal 3). In each model, the observation component operates by return year, accounting for measurement error associated with abundance estimates and scale samples from the harvest and escapement.

Goal 1: The conspicuously high jack proportions that motivated this study have occurred in the return year age composition, where jacks have comprised almost half of total (male plus female) runs in some years. To detect potentially less obvious temporal patterns in the proportion of individuals maturing as jacks within cohorts, we fit a biased (i.e., containing a linear trend) random walk to the time-series of logit jack proportions by brood year based on values from the ADF&G run reconstruction:

$$\begin{aligned} J_y &= J_{y-1} + u + w_y \\ w_y &\sim N(0, \sigma_{error}) \end{aligned} \tag{2.1}$$

where (J_y) represents the predicted logit jack proportion in brood year y, w_y is a normally distributed error term, and u is a logit-linear trend parameter. The standard deviation of the error terms σ_{error} was drawn from a half-Cauchy prior distribution with a location of 0 and a scale of 2.5 (Anderson, Branch, Cooper, & Dulvy, 2017), and the linear trend term (u) was drawn from a normal prior distribution with a mean of 0 and a standard deviation of 10. This model form was also fitted to the time-series of jack and non-jack log abundances by brood year (also generated from the ADF&G run reconstruction) to compare temporal patterns in jack prevalence to variation in the returns of older individuals.

Goal 2: To identify environmental and demographic factors influential to the proportion of individuals maturing as jacks within cohorts**,** logit jack proportions (J_y) across brood years were modeled as a lag-1 autoregressive (AR(1)) process of the form:

$$\begin{gathered} J_y = \mu_J + \phi(J_{y-1} - \mu_J) + \boldsymbol{b} \cdot \boldsymbol{c}_y + w_y \\ w_y \sim N(0, \sigma_{proc}) \end{gathered} \tag{2.2}$$

In this equation, ϕ describes the autocorrelation in the state, μ_J represents the mean of the time series, $\boldsymbol{c}_y$ is a vector of covariate values for brood year y that affect the state, $\boldsymbol{b}$ is a vector of coefficients that describe the effect of each covariate, and the w_y are normally distributed process errors. We chose an AR(1) model based on inspection of autocorrelation in the raw data, and the expectation that low-frequency environmental variation influencing juvenile growth and body condition would manifest as lag-1 autocorrelation in the time-series. Covariates evaluated for their effects on jack prevalence in a given cohort included the logit observed jack proportion in the males that sired that cohort, the log observed abundance of females that spawned that cohort (a proxy for rearing density, Schindler, Rogers, Scheuerell, & Abrey, 2005), the annual NPGO index, annual Kodiak air temperatures, and the log biomass of cladoceran zooplankton in Frazer Lake. The jack proportion and abundance of females in the spawners were each based on annual weir censuses of returning fish (see Methods: Data Collection). The effect of NPGO was considered as a two-year moving average, shifted forward by two and three years to encompass the window in which most fish from a given brood year would migrate to the ocean. Kodiak air temperature and Frazer Lake zooplankton biomass were both specified as two-year moving averages, shifted forward by one and two years to capture the period in which most fish from a given cohort would rear in the lake. Alternative reasonable combinations of lags and moving average lengths did not qualitatively alter model outcomes (Appendix B, Fig. B1). All model coefficients $(\boldsymbol{b})$ were drawn from (assumed) vague normal prior distributions with means of zero and standard deviations of 10, and all covariates were Z-scored. Phi (ϕ) was drawn from a uniform prior distribution with limits -0.999 to 0.999, μ_J was drawn from a normal prior distribution with a mean of 0 and a standard deviation of 20, and the process error standard deviation (σ_{proc}) was drawn from a half-Cauchy prior distribution with a location of 0 and scale of 2.5 (Anderson et al., 2017).

The information available for estimating brood year jack proportions are the scale samples and count data collected each return year from the harvest and escapement (See Methods: Data Collection). As such, model predictions of abundance and age composition for each of these sample sources needed to be generated from eq. 2 to evaluate the appropriate likelihoods. To do so, first the abundance of jacks (B_y^J) and non-jacks (B_y^H) were calculated from the estimated logit jack proportions (J_y), and the abundance of the total return (B_y):

$$\begin{aligned} B_y^J &= B_y \frac{e^{J_y}}{1+e^{J_y}} \\ B_y^H &= B_y - B_y^J \end{aligned} \tag{2.3}$$

The return to brood year y (B_y) was modeled as a function of the total spawner abundance in that year (S_y) according to the Ricker spawner-recruit relationship (Ricker, 1954):

$$\begin{aligned} \ln(B_y) &= \ln(S_y) + \ln(\alpha) - \beta S_y + w_y \\ w_y &\sim N(0,\sigma_R) \end{aligned} \tag{2.4}$$

where α is the productivity parameter and β is the inverse capacity term of the Ricker function, and the w_y are independent, normally distributed process errors. The broad uniform distributions that serve as reference priors for the Ricker spawner-recruit parameters (Millar, 2002) can be problematic for posterior sampling, so we used weakly informative priors for these terms based on estimates from other Kodiak sockeye salmon populations (Polum, Evans, & Dann, 2014; Schaberg, Foster, Wattum, & McKinley, 2016). Log productivity $(\ln(\alpha))$ and inverse capacity (β) were drawn from normal prior distributions with means of 0 and standard deviations of 20 and 0.1 respectively, and σ_R was drawn from a half-Cauchy prior distribution with a location of 0 and a scale of 2.5. While the AR(1) form of the Ricker is commonly used for Alaskan salmon, we found no evidence of autocorrelation in the state residuals for eq. 4.

Numbers at age by brood year $(B_{y,a})$ were developed by multiplying the abundances of jacks and non-jacks by their respective maturity schedules:

$$B_{y,a\in A^k} = B_y^k p_{y,a}^k \tag{2.5}$$

Here, k identifies whether a certain quantity pertains to jacks $(k = J)$ or non-jacks $(k = H)$ and a represents unique combinations of freshwater and marine ages. For simplicity, a is indexed numerically (e.g. $a = 1$ represents ocean age-1, freshwater age-1, $a = 2$ represents ocean age-1, freshwater age-2 etc.). A^k denotes the set of age classes possible for jacks $(A^J = 1:3$, representing ocean age-1, freshwater ages-1:3$)$ and non-jacks $(A^H = 4:9$, representing ocean ages 2-3, freshwater ages-1:3$)$. Brood year age composition proportions for jacks and non-jacks were drawn from separate Dirichlet prior distributions, implemented as vectors of independent gamma-distributed variables $(\lambda_{y,a})$ divided by their sums (Gelman et al., 2013).

$$p_{y,a}^{k} = \frac{\lambda_{y,a}}{\sum_{a=A_{\delta}^{k}}^{A_{\omega}^{k}} \lambda_{y,a}}$$

$$\lambda_{y,a} \sim Gamma(\alpha = \xi_a, \beta = 1) \tag{2.6}$$

where $a \in A^k$, and A_δ^k and A_ω^k are the first and last elements of A^k ($A_\delta^J = 1$, $A_\omega^J = 3$, and $A_\delta^H = 4$, $A_\omega^H = 9$). In this parameterization of the gamma distribution, the inverse scale (rate) term (β) is a scaling factor that affects neither the mean nor the variability of the distribution, and was fixed at 1 following Fleischman et al. (2013). Values of ξ_a were themselves drawn from vague gamma prior distributions with α = 0.001 and β = 0.001.

Numbers-at-age by return year were constructed by specifying the abundance of fish of age class a in return year t as the number of fish of age class a originating from brood year $y = t - T_a$, where T_a represents the total age (gravel year plus freshwater and ocean ages) of age class a.

$$R_{t,a} = B_{y=t-T_a,a} \tag{2.7}$$

These values were then partitioned into numbers-at-age in the harvest (C) and escapement (E) according to age-specific annual exploitation rates $(u_{t,a})$.

$$
\begin{aligned}
R_{t,a}^{C} &= R_{t,a} u_{t,a} \\
R_{t,a}^{E} &= R_{t,a} - R_{t,a}^{C}
\end{aligned}
\tag{2.8}
$$

where $u_{t,a}$ were drawn from vague beta prior distributions:

$$u_{t,a} \sim Beta(0.5,0.5) \tag{2.9}$$

Goal 3: Because salmon acquire the majority of their adult body mass at sea, duration of marine residency is a particularly informative descriptor of a population's age structure. To estimate the degree of variability and coherence in the dynamics of the Frazer Lake population's main ocean age classes, we modeled their abundances by brood versus return year as two separate multivariate processes of the form:

$$
\begin{aligned}
\boldsymbol{x}_y &= \boldsymbol{x}_{y-1} + \boldsymbol{w}_y \\
\boldsymbol{w}_y &\sim MVN(0, \boldsymbol{Q}_{brood})
\end{aligned}
\tag{2.10}
$$

$$
\begin{aligned}
\boldsymbol{x}_t &= \boldsymbol{x}_{t-1} + \boldsymbol{w}_t \\
\boldsymbol{w}_t &\sim MVN(0, \boldsymbol{Q}_{return})
\end{aligned}
\tag{2.11}
$$

where $\boldsymbol{x}_y$ and $\boldsymbol{x}_t$ represent state vectors of the log abundance of ocean age-1, 2, and 3 fish in brood year y and return year t respectively. Process errors $(\boldsymbol{w}_y, \boldsymbol{w}_t)$ were assumed to be multivariate normally distributed with a mean of 0 and a variance-covariance matrix $\boldsymbol{Q}$. To estimate the degree of temporal coherence in the abundance of different ocean age classes by brood versus return year, we assumed a variance-covariance matrix structure with equal variance, and a single covariance term (γ) as an estimated parameter (i.e. variance (σ^2_{proc}) on the diagonal of the matrix, and a single covariance term (γ) on all other entries). To avoid parameter draws leading to non-positive definite matrices, γ was specified as the product of the variance (σ^2_{proc}) and the correlation (ρ) of the $\boldsymbol{Q}$ matrix. The process error standard deviation (σ_{proc}) was drawn from a half-Cauchy prior distribution with a location of 0 and a scale of 2.5, and ρ was drawn from a uniform prior distribution with limits of -0.999 to 0.999. Alternative methods to quantify synchrony among age classes by brood versus return year using cross-correlation yielded qualitatively similar results (Appendix B, Fig. B2).

For each ocean age, its abundance ($e^{\boldsymbol{x}^i}$, where i = ocean age 1, 2 or 3) was multiplied by its freshwater age composition proportions $(\boldsymbol{p}_a^i)$ to calculate numbers-at-age. For the model represented by eq. 10, this calculation generated numbers-at-age by brood year:

$$B_{y,a\in A^i} = e^{x_y^i} p_{y,a}^i \tag{2.12}$$

For the model represented by eq. 11, this calculation produced estimates of numbers-at-age by return year:

$$R_{t,a\in A^i} = e^{x_t^i} p_{t,a}^i \tag{2.13}$$

In each equation, A^i represents the set of specific age classes comprising a given ocean age (i.e., freshwater ages; $A^{i=1} = 1:3$, representing ocean-age-1, freshwater-ages-1:3, $A^{i=2} = 4:6$, representing ocean-age-2, freshwater-ages-1:3 etc.). Proportions-at-freshwater age for each marine age class were drawn from separate Dirichlet prior distributions, implemented as in eq. 6. For the brood year model (eq. 10), estimates of numbers-at-age by return year were calculated as in eq. 7. In both models, numbers-at-age in the run were assigned to the harvest or escapement as in eq. 8.

For all process models (goals 2, 3), in each return year (t), the likelihoods for the abundance of Frazer Lake sockeye salmon in the harvest and escapement were assumed to follow log-normally distributed observation processes.

$$N_t^s \sim Lognormal(\mu_s = \ln\sum_{a=1}^{\omega} R_{t,a}^s, \sigma_s) \tag{2.14}$$

where ω represents the total number of all age classes (a) included in the analysis, $\ln\sum_{a=1}^{\omega} R_{t,a}^s$ are the model-predicted estimates of the log abundance of fish in return year t within a given sample source s, where $s = \text{catch}(C)$ or $\text{escapement}(E)$, and N_t^s are the observed counts. Simultaneous estimation of process and observation error variance led to unresolvable divergent transitions during sampling (Betancourt, 2016; Monnahan, Thorson, & Branch, 2017), so we fixed the log-normal observation error terms for the catch (σ_C) and escapement (σ_E) at 0.5 and 0.1 respectively, following a generalized run reconstruction model recently developed by Cunningham et al. (2017) that was applied to sockeye salmon in Bristol Bay, Alaska. Alternative values of these parameters did not qualitatively alter model outcomes (Appendix B, Fig. B3-B5).

Numbers-at-age observed in the scale samples taken from the harvest $(\boldsymbol{z}^C)$ and escapement $(\boldsymbol{z}^E)$ were assumed to follow a multinomial error structure. Scales were not collected from the harvest in certain years due to small run sizes and limited fishing, so age composition likelihoods for a given sample source were only evaluated for the subset of years in which data were available (V^s).

$$\begin{gathered}\boldsymbol{z}^s_{t \in V^s} \sim Multinomial(\varepsilon_t^s, \boldsymbol{\theta}_t^s) \\ \theta_{t,a}^s = \frac{R_{t,a}^s}{\sum_{a=1}^{\omega} R_{t,a}^s}\end{gathered} \tag{2.15}$$

where $\boldsymbol{\theta}_t^s$ are vectors of model-predicted annual age composition proportions calculated from the numbers-at-age estimates $(R_{t,a}^s)$ and ε_t^s are the effective sample sizes from a given source.

We fixed ε_t^s to be the minimum between each year's actual sample size or 1,000 for both the harvest and escapement (Fournier, Hampton, & Sibert, 1998).

In all models, posterior sampling was achieved via Hamiltonian Monte Carlo (HMC) routines executed in Stan (Stan Development Team, 2015) and implemented in R (R Core Team, 2015) using the Rstan package (Guo et al., 2016). Sampling occurred over four chains of 30,000 iterations each, with the first half of samples discarded as a 'warmup' and one out of every five subsequent samples saved to develop the posterior distribution. Convergence was assessed using the Gelman-Rubin diagnostic (Gelman & Rubin, 1992) and effective number of samples, as well as trace-plots and autocorrelation plots of HMC chains. Posterior sampling was monitored for divergent transitions and low Bayesian Fraction of Missing Information (BFMI), neither of which were indicated. For all models, goodness of fit was assessed by comparing predictive distributions to observed data (posterior predictive checks; Appendix B, Fig. B6-B8), parameter estimation was validated using simulated data (Appendix B, Fig. B9-B11), and both state (process) and model (observation) residuals were examined for non-stationarity and autocorrelation, neither of which were evident.

2.4 RESULTS

From brood years 1968 to 2008, the proportion of Frazer Lake sockeye salmon maturing as jacks exhibited a positive shift (Fig. 2.2A). Jack proportions within cohorts (i.e., the age composition of returns from a given brood) increased from an average of ~0.05 in the first half of this time period to ~0.09 in the latter half. The posterior median of the trend term (u , eq. 1) in the biased random walk fitted to the logit of these data was 0.03 year^{-1}, with a 95% credible interval of 0.01 to 0.05 year^{-1} (Fig. 2.2D). This increase in jack proportions reflects a positive trend in the abundance of jacks within the population as well (u median = 0.05, 95% credible interval = 0.03 to 0.08 log abundance year^{-1}) (Fig. 2.2B, E). Interestingly, jack proportions were high from 1969 to 1974 (Fig. 2.2A) when the Frazer Lake stock was still in the process of becoming established and total returns were relatively weak (Fig. 2.2B, C). While there is evidence of a slight positive trend in non-jack returns from brood years 1968 to 2008 (u, median = 0.03, 95% credible interval 0.00 to 0.05 log abundance year^{-1}) (Fig. 2.2C, F), non-jack abundance has exhibited a steady decline since the peak recruitment event of 1986 (Fig. 2.2C). Model fits to this subset of data (not shown) indicated a median value for u of −0.05, with a 95% credible interval of −0.1 to −0.01 log abundance year^{-1}.

We found little evidence for any effect of environmental variation on the proportion of individuals maturing as jacks within cohorts. The coefficients for annual NPGO (median = 0.01, 95% credible interval = −0.32 to 0.31), air temperature (median = 0.05, 95% credible interval = −0.38 to 0.48), and log cladoceran zooplankton biomass in Frazer Lake (median = −0.05, 95% credible interval = −0.44 to 0.31) each suggested no consistent association with a cohort's jack prevalence. Similarly, there was limited support for a relationship between the log abundance of females in the breeding population (a proxy for fry production and rearing density (Schindler et al., 2005)) and the prevalence of jacks in the ensuing year-class (median = −0.12, 95% credible interval = −0.52 to 0.22). However, the jack proportion in the return from a given brood year exhibited a strong, positive association with the prevalence of jacks among the males that sired that cohort (median = 0.43, 95% credible interval = 0.04 to 0.77) (Fig. 2.3, 2.4). The effect of this covariate was by far the largest among those considered (Fig 3B).

Estimates of Frazer Lake sockeye salmon abundance by brood year indicated substantial interannual variation in cohort strength for this population (Fig. 2.5B; median σ_R = 0.83, 95% credible interval = 0.64 to 1.12). Year-to-year variation in abundance was synchronous among marine age classes by brood year (γ_{brood}, median =1.16, 95% credible interval = 0.67 to 2.11), but distinctly asynchronous by return year (γ_{return}, median = -0.25, 95% credible interval = -0.56 to 0.06) (Fig. 2.5C, F). Return year dynamics appear uncorrelated throughout the time-series, although the magnitude of this asynchrony increased conspicuously in 2003 (Fig. 2.5E). This increase was initiated by two consecutive poor recruitments from the 1997 and 1998 brood years, followed by stronger recruitment from the 1999 brood year (Fig. 2.5B). Most Frazer Lake sockeye salmon spend two years in the lake after overwintering in the gravel, such that the most common total ages for jacks, ocean age-2, and ocean age-3 fish are four, five, and six years respectively. Consequently, most ocean age-2 and ocean age-3 fish produced from the weak 1998 and 1997 brood years returned to spawn in 2003, together with jacks from the much stronger 1999 year-class, resulting in approximately 45% of the 2003 run being composed of jacks. Similar, though less conspicuous 'cohort mismatches' occurred in each return year characterized by high jack prevalence throughout the population's history (e.g. 1996, 1999, 2002, 2007, 2010, 2011, Fig. 2.5B, D, E).

From 1986 to 2015, median posterior estimates of annual exploitation rates for ocean age-2 and ocean age-3 fish averaged 0.52 and 0.60 respectively, while jacks were subject to average harvest rates of only 0.13 (Fig. 2.6D). As a result, in years when jacks made up a large share of the total run, they usually comprised an even greater portion of the spawning escapement (Fig. 2.6A-C). Moreover, while our harvest estimates were not stratified by sex, similar studies in other regions have identified greater fishery selectivity for (non-jack) male versus female sockeye salmon (Kendall & Quinn, 2013). For instance, in 2003, while jacks comprised roughly 45% of the total run, they accounted for 53% of the escapement and almost 70% of spawning males, even with a relatively low harvest rate (~ 0.22) on ocean age-2 fish in that year (Fig. 2.5D, Fig. 2.6A, B, D).

2.5 DISCUSSION:

Our results indicate a distinct increase in the proportion of Frazer Lake sockeye salmon maturing as jacks between brood years 1968 and 2008. Temporal fluctuations in jack prevalence observed in other salmon populations have been attributed to environmental variation (Koseki & Fleming, 2007). The putative mechanism behind this association is that variation in factors influencing food availability, juvenile metabolism, or rearing density can affect the proportion of individuals reaching the growth/lipid accumulation threshold necessary for early maturation (Gross, 1991; Shearer & Swanson, 2000; Thorpe et al., 1998). Hatchery operations are thought to influence jacking rates as well, both through enhancing the growth and body condition of hatchery-reared juveniles, and unintentional selection for younger age-at-maturity (Hankin, Fitzgibbons, & Chen, 2009; Unwin & Glova, 1997). However, we found little evidence for an association between the proportion of fish maturing as jacks and food availability, temperature, or variation in the marine environment relevant to salmon productivity, and limited support for an effect of rearing density. Moreover, the Frazer Lake stock is an entirely wild-spawning (albeit introduced) population, and most hatchery propagation of sockeye salmon on Kodiak Island occurs near Spiridon Bay (Thomsen & Schrof, 2009), over 100 miles around the coast from Frazer Lake (Fig. 2.1B). Instead, we found a strong positive relationship between the proportion of spawning males that were jacks, and the proportion of individuals maturing as jacks in the ensuing cohort, suggesting that genetic factors are important in the determination of an individual's reproductive life history. This association is consistent with results from controlled breeding experiments that have demonstrated heritability ($h^2 \sim 0.3$-0.6) of the jack life history in other salmon species (Hankin et al., 1993; Heath, Rankin, Bryden, Heath, & Shrimpton, 2002; Heath, Devlin, Heath, & Iwama, 1994) as well as evidence from hatchery augmentation research (Unwin & Glova, 1997). While previous studies have indicated that the mating success of jacks is negatively frequency-dependent (owing to greater competition for sneaking opportunities and refugia when jacks are common (Berejikian et al., 2010; Gross, 1984, 1985)), it is important to note that even if the average reproductive success of a phenotype declines at higher frequencies, the total share of fertilizations obtained by that tactic collectively can still increase as it becomes more prevalent (Ayala & Campbell, 1974). Our results suggest that this is likely the case for jacks in Frazer Lake sockeye salmon, at least over the range of values observed in this study (Fig. 2.4).

Parental factors may strongly influence the proportion of individuals maturing as jacks in a given cohort, but this alone cannot explain why such proportions have increased over time. In fact, it is only when alternative tactics are genetically-based that FDS is expected to stabilize their frequencies (Shuster & Wade, 2003; Taborsky, Oliveira, & Brockmann, 2008). However, our analysis suggests that the volatile recruitment dynamics of Frazer Lake sockeye salmon may act to disrupt the stabilizing influence of FDS on this population's tactic frequencies. This is due to the fact that jacks and hooknose males differ in age-at-maturity, such that individuals of each phenotype co-occurring on the spawning grounds are products of different cohorts. Because interannual variation in survivorship is synchronous within year-classes, the ratio of jacks to hooknoses in the spawning population necessarily varies based on their relative cohort sizes. A similar pattern was described in Coho salmon (*O. kisutch,* Walbaum 1792) by Koseki & Fleming (2006), who noted that the difference in age-at-maturity between male phenotypes decoupled their synchronous fluctuations in abundance within cohorts. Our results show that when recruitment is highly variable, jacks from strong year-classes may often spawn among older males from the much weaker recruitments of earlier brood years, leading to 'cohort mismatches' in the breeding population that would not occur if recruitment were more stable. Consequently, jacks can repeatedly achieve substantial representation in the spawning population and subsequently high total fertilizations, increasing the prevalence of jacks in the next generation as well. These cohort mismatches are clearly responsible for the unusually high jack proportions observed in Frazer Lake sockeye runs by return year, and are likely contributing to the increasing proportion of individuals maturing as jacks within year classes as well.

The variable population dynamics of Frazer Lake sockeye salmon may be caused or compounded by the unusual history of this population. Sockeye salmon were introduced into Frazer Lake less than seventy years ago using broodstock from neighboring populations (Ayakulik/Red Lake, Karluk Lake, Fig 1C), as well as Ruth Lake/Lake Becharof on the Alaska Peninsula (Fig. 2.1B). Due to their philopatric life history, anadromous salmonids typically exhibit fine-scale local adaptation to their natal habitats (Quinn, 2005). As the relatively recent descendants of individuals from populations that evolved in foreign environments, Frazer Lake fish may lack the same degree of local adaptation seen in other stocks, potentially leading to high variability in survivorship. We found synchronous patterns of abundance within year-classes, indicating that survivorship is established in the freshwater or early marine phase of life, when individuals from a given cohort are exposed to common environmental conditions. It is primarily to the freshwater environment that local adaptation is thought to occur (but see Johnson &

Schindler, 2013), such that incomplete adaptation to the Frazer Lake system may be contributing to the high variability in survivorship that this population exhibits. Indeed, noting substantial temporal variation in the spawning distribution, age composition, and abundance of Frazer Lake sockeye salmon, Burger et al. (2000) suggested that the population had not yet reached genetic or demographic equilibrium. As such, it is plausible that stochastic recruitment has not perturbed the Frazer Lake population's tactic frequencies away from an existing evolutionary equilibrium, but rather may have disrupted the development of any such equilibrium to begin with.

In addition to recruitment variability, there are other factors that have likely contributed to the increased prevalence of jacks in Frazer Lake sockeye salmon. Most notably, it is clear that fishery exploitation rates have been substantially lower for jacks than for ocean age-2 or ocean age-3 fish throughout most of the population's history. This is not unexpected, as Frazer-bound fish are harvested primarily in a terminal gillnet fishery, which is strongly size-selective (depending on the mesh sizes used; Foster, 2014). Indeed, analyses of the gillnet fishery for sockeye salmon in Bristol Bay, Alaska, showed disproportionate exploitation rates on older, larger individuals (Kendall & Quinn, 2009). Thus, in years when jacks from strong recruitments return to spawn among older males from weaker year-classes, the numerical discrepancy in cohort sizes will be amplified by greater harvest of older individuals. Similarly, even in years when jacks are not a large portion of the total run, they may still comprise a substantial proportion of the spawning escapement due to size-selective harvest. However, there are gillnet fisheries for sockeye salmon throughout Alaska, and the exploitation rates of Frazer Lake fish are similar to those in other regions (Kendall & Quinn, 2009). Yet, to our knowledge, increases in jack prevalence of the magnitude seen in Frazer Lake have not been documented in any other Alaskan sockeye salmon population (DeFilippo et al., 2018; ADF&G unpublished data).

Furthermore, many years in which jacks comprised a large portion of the spawning escapement to Frazer Lake were also years with some of the lowest exploitation rates on older individuals (e.g. 2003, 2007, 2010; Fig. 2.6). As such, it is unlikely that size-selective harvest alone is responsible for the observed rise in jack prevalence, although it is likely a contributing factor.

While our analysis indicates that heritability of the jack life history, coupled with recruitment variation and size-selective harvest are responsible for the rising prevalence of jacks in Frazer Lake sockeye, there are alternative mechanisms that merit consideration. Our results suggest that enhanced jack prevalence in the breeding population arising from cohort mismatches leads to a high proportion of jacks in the ensuing cohort, which we attribute to the heritability of the jack life history. However, runs that exhibit cohort mismatches on the spawning grounds also tend to be relatively weak owing to reduced representation of older age classes that are usually numerically dominant. Therefore, cohorts resulting from these breeding events could be more likely to produce jacks due to reduced spawner abundance, fry production, and density-dependent competition among juveniles. Such reduced density-dependence could enhance juvenile growth and body condition within a cohort such that more individuals are likely to mature as jacks, creating a spurious association between the prevalence of jacks in the spawning population and its offspring. We included female spawning abundance as a covariate in our model to account for this possibility, the effect of which was much weaker than the prevalence of jacks in the breeding population. Nonetheless, the effect of rearing density was predominantly negative as expected, and stronger than any of the environmental variables considered. As such, it is possible that reduced density dependence may be contributing to the effects of cohort mismatches in the breeding population on the prevalence of jacks in the next generation, in conjunction with the heritability of the jack life history. However, while total run size fluctuates, the fixed escapement policy under which the Frazer Lake population is managed may dampen any density-dependent effects on jack prevalence. In addition, it is worth noting that while the primary donor population to Frazer Lake (Ayakulik) has not shown any apparent shifts in jack prevalence, it does exhibit jack proportions that are relatively high compared to other Alaskan sockeye salmon stocks (Appendix B, Fig. B12; DeFilippo et al., 2018). As such, Frazer Lake fish may have been predisposed towards high jacking rates due to their ancestry, although this alone cannot explain the increased prevalence of jacks in recent decades.

The nutrient fertilization of Frazer Lake may also have contributed to the rise in this population's jack prevalence. Such an effect would presumably occur via an increase in ecosystem primary productivity, zooplankton biomass, and subsequently, juvenile growth and body condition. However, we found no evidence of a relationship between zooplankton biomass and jack prevalence among cohorts. While there were pronounced increases in jack proportions within the 1991 and 1992 year-classes (Fig. 2.2A), which were likely exposed to the effects of fertilization, closer examination of the data shows elevated jack proportions in the spawners that sired these cohorts (Fig. 2.3A), owing to variable recruitment dynamics and size-selective harvest (Appendix B, Fig. B13; Fig. 2.6D). Moreover, the fertilization of Frazer Lake only occurred from 1988 to 1992, and it is unlikely that this brief episode could be responsible for the rising prevalence of jacks in recent years. Nutrient fertilization campaigns of sockeye salmon rearing lakes were historically numerous, and the results of these efforts have been described in great detail (see Barraclough & Robinson, 1972; Budy, Luecke, & Wurtsbaugh, 1998; Hilborn & Winton, 1993; Hyatt, McQueen, Shortreed, & Rankin, 2004; Hyatt & Stockner, 1985; Kyle, 1994; Lebrasseur et al., 1978; Mazumder & Edmundson, 2002). However, despite such intensive study, to our knowledge there is no published account of a similar shift in jack prevalence following the nutrient fertilization of a sockeye salmon nursery lake.

It is not clear how the distribution of alternative male phenotypes in Frazer Lake sockeye salmon will behave in the future, but it seems unlikely that FDS could maintain a stable equilibrium in this stock so long as current levels of recruitment stochasticity persist. Importantly, substantial fluctuations in year-class strength occur in many salmon populations (White, Botsford, Hastings, & Holland, 2014), suggesting that stable equilibria between alternative life histories may be difficult to achieve in other stocks as well. The heritable trait through which FDS operates in salmon is likely the growth or lipid accumulation threshold for precocious maturation (Gross, 1991; Shearer & Swanson, 2000). As such, the relative reproductive success of a tactic should also determine the proportion of offspring inheriting maturation threhsolds that will dispose them towards expressing that tactic (Hankin et al., 1993). Repeated over generations, this process can produce an evolutionarily stable distribution of threshold genotypes that reflects the frequency-dependent fitness functions of alternative tactics (Hutchings & Myers, 1994; Shuster & Wade, 2003). Importantly, this mechanism assumes that the ratio of male phenotypes on the spawning grounds reflects the current distribution of threshold values in the population. However, if the ratio of jacks to hooknoses in the breeding population each year depends more on their respective cohort sizes, as our results suggest, then the frequency-dependent mating success of individuals will be effectively decoupled from their maturation decisions, causing the fitness payoffs associated with a particular threshold value to vary over time. As Koseki & Fleming (2006) noted, this dynamic should make an evolutionary equilibrium between male phenotypes more difficult to achieve. Our results support this assertion, suggesting that unless recruitment is constant over time, the ratio of male mating phenotypes in the breeding population will be repeatedly perturbed — each time affecting the distribution of threshold values, and ultimately tactic frequencies in the ensuing cohort (Hankin et al., 1993). Consequently, the realized frequencies of alternative male phenotypes in some populations may reflect the magnitude and pattern of these perturbations rather than the conditions of a stable equilibrium maintained by FDS, such that jacks would be more common in stocks with highly variable dynamics. While we were able to observe a discernable shift in tactic frequencies associated with recruitment variation in Frazer Lake sockeye salmon, this is likely a product of the unique opportunity presented by this stock to observe the development of a nascent population.

This study contributes to a growing body of work emphasizing the importance of evolutionary factors in the management of exploited populations (Allendorf & Hard, 2009; Heino et al., 2013; Heino, Díaz Pauli, & Dieckmann, 2015; Kendall, Dieckmann, Heino, Punt, & Quinn, 2014; Kuparinen & Hutchings, 2016; Kuparinen & Merilä, 2007). Most studies on harvest-induced evolution have focused on continuous life history traits (e.g. size and age-at-maturity), while consideration of discontinuous variation (i.e. alternative maturation/reproductive phenotypes) is comparatively scarce, despite the large effects such variation can have on population age/size structure and fishery performance (Larsen et al., 2004; Myers, 1984; Zimmerman et al., 2003). Our findings suggest that genetic factors are important in the determination of an individual's mating phenotype, such that exploitation methods consistently targeting larger, older salmon may lead to selection in favor of jacks. Moreover, our study indicates that recruitment variation can lead to cohort mismatches in the breeding population that override the stabilizing effects of FDS, and increase the total fertilizations obtained by jacks beyond what would be expected under equilibrium conditions. As such, managers seeking to control the prevalence of jacks in highly variable populations may need to develop methods to limit their presence on the spawning grounds. Increasing exploitation rates on jacks by using harvest methods that are less size-selective may be one way to achieve this. Alternatively, the development of passive mechanisms to exclude some jacks from the spawning grounds that are not as financially or logistically demanding as culling may also be viable. Stabilizing population dynamics is likely to be the most effective management solution (avoiding both the high jack proportions in the run, and in the ensuing cohort), but also the least realistic to implement. Indeed, understanding the causes of variation in fish populations is a fundamental goal of fisheries science (Sissenwine, 1984; Smith, 1994), and it may be safely assumed that stocks would be managed to minimize variability if scientists knew how to accomplish this. Nonetheless, biologists have identified several anthropogenic factors that can amplify population variability, such as high exploitation rates (Essington et al., 2015; Hsieh et al., 2006; Shelton & Mangel, 2011), and reduced biocomplexity (Carlson & Satterthwaite, 2011; Griffiths et al., 2014; Moore, Mcclure, Rogers, & Schindler, 2010). Managing stocks with these factors in mind may be useful in minimizing variability and avoiding the undesirable proliferation of jacks. However, sources of variation differ between populations (Szuwalski, Vert-Pre, Punt, Branch, & Hilborn, 2015; Vert-pre, Amoroso, Jensen, & Hilborn, 2013) and identifying the drivers of demographic variability specific to a given stock will likely be necessary to develop effective management approaches for stabilizing its dynamics.

2.6 FIGURES

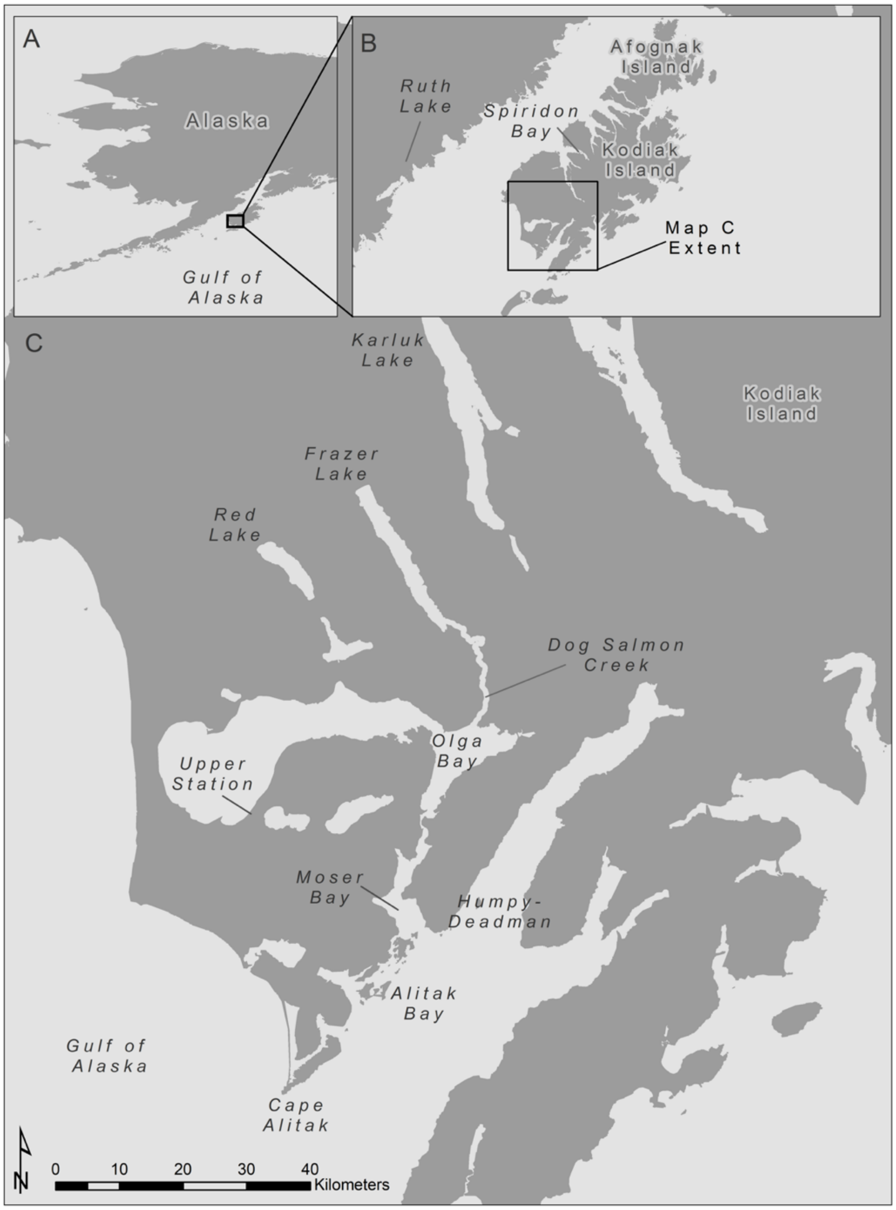

Figure 2.1. Map of Kodiak Island, with Frazer Lake and its associated donor lakes, harvest areas, and other relevant locations indicated.

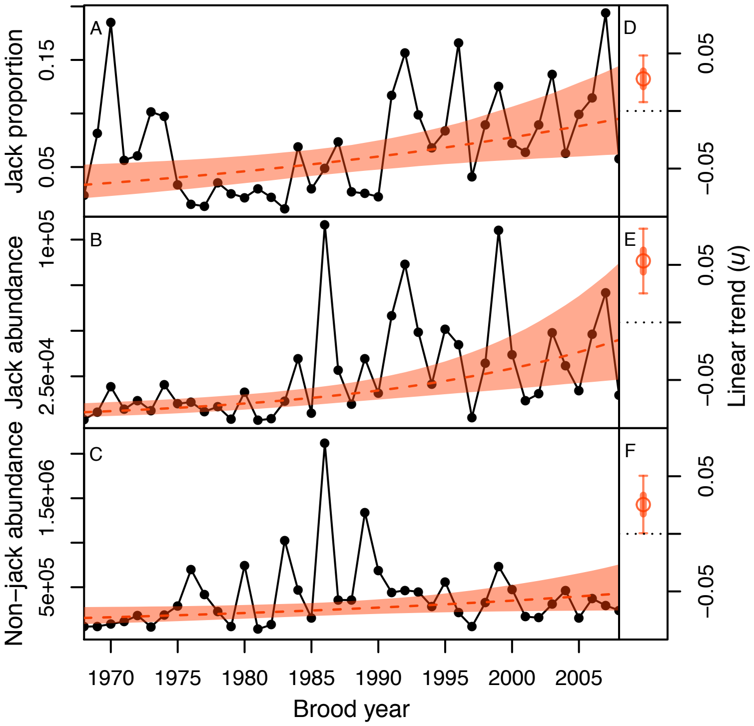

Figure 2.2. Time-series of jack proportions (A), jack abundance (B) and non-jack abundance (C) within cohorts. Data (based on calculations from the ADF&G run reconstruction) are shown as black dots and lines, while model predictions from a biased random walk fitted to these data are shown in orange. Median posterior estimates are shown as dashed orange lines, with the 95% credible intervals depicted in transparent orange. The right-hand panels depict the posterior distribution of the trend term (u) from model fits to brood year jack proportions (D), jack abundance (E), and non-jack abundance (F). Circles represent the median values of the posterior distributions, and thick and thin lines represent the 50% and 95% credible intervals respectively.

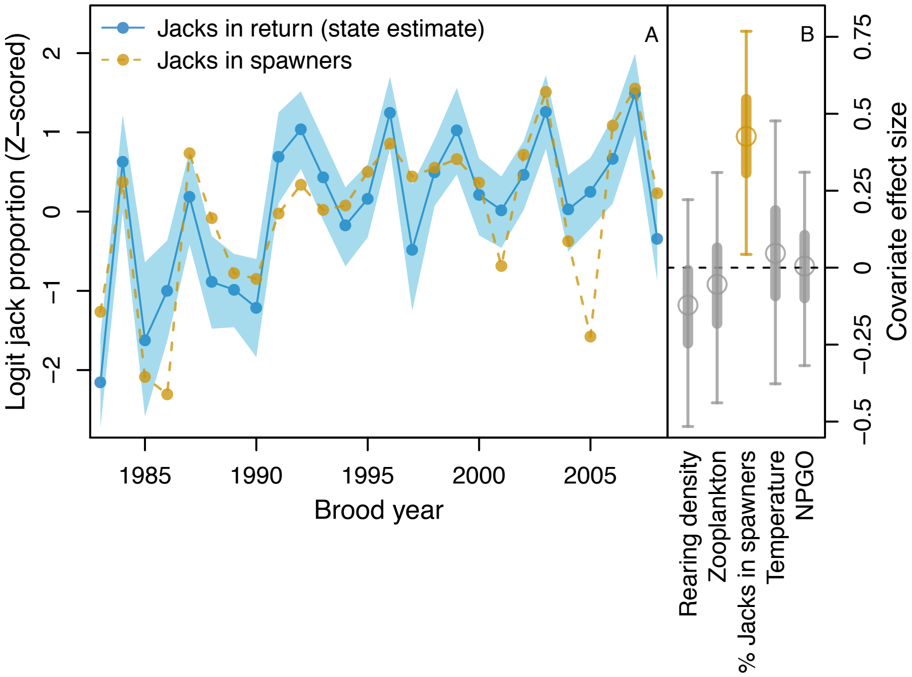

Figure 2.3. Covariate effects on jack prevalence within cohorts. Panel A depicts the model-predicted estimates of jack proportions within the return from each brood year (blue). The median is represented by the solid line and points, and the 95% credible interval is indicated by the transparent boundary. Posterior distributions for the coefficients of all Z-scored covariates that were evaluated are depicted in panel B, with the medians shown as circles, and the 50% and 95% credible intervals depicted as thick and thin lines respectively. The posterior distribution for the covariate with the largest effect (proportion of spawning males that were jacks) is colored gold, and the time series for this variable is plotted alongside the state estimate to illustrate the relationship between these two variables. Note: jack proportions in the return are Z-scored here to be on the same scale as the covariates, but in the fitted model they were not.

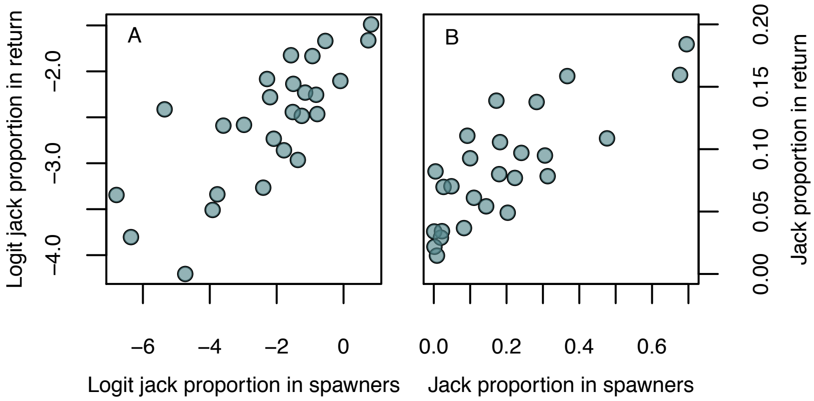

Figure 2.4. Spawner-return relationships for jack prevalence. The y and x axes depict jack proportions in the return and the spawners respectively, in logit (A) and linear (B) space.

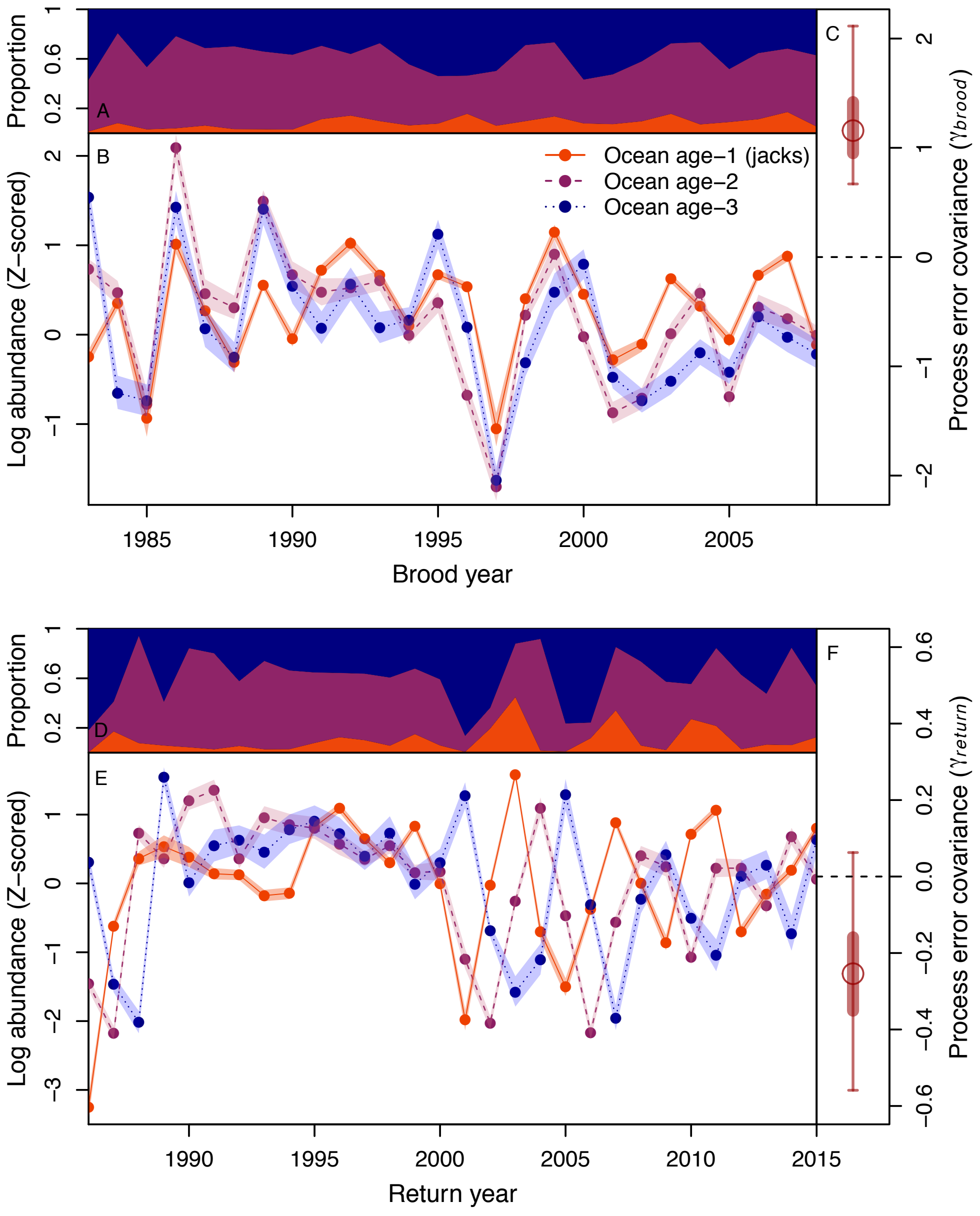

Figure 2.5. Temporal patterns in the marine age composition of the total (harvest plus escapement) population by brood and return year. Panels A and D show the posterior median estimates of the proportions of Frazer Lake sockeye salmon of ocean age-1, 2, and 3 by brood year (A) and return year (D). Panels B and E depict Z-scored state estimates of the log abundance of ocean age-1, 2, and 3 fish by brood year (B) versus return year (E). Posterior medians are indicated by solid dots, while the 50% credible intervals are indicated as transparent

boundaries. Panels C and F depict the posterior distribution of the process error covariance (γ) for each multivariate time series. The posterior median is indicated by a circle, while the 50% and 95% credible intervals are represented by thick and thin lines respectively.

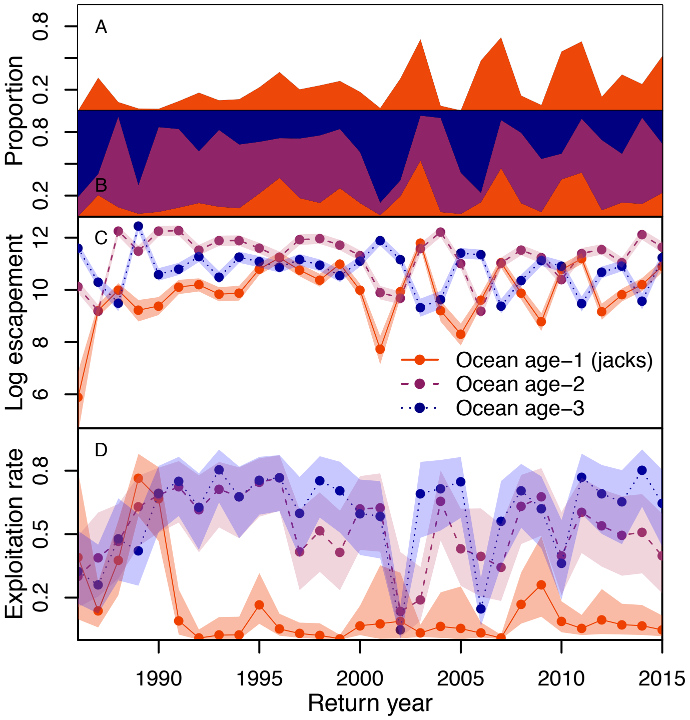

Figure 2.6. Estimated harvest rates and prevalence in the spawning escapement by ocean age. Panel A depicts the proportion of males in the escapement that were jacks (based on visual identification during annual weir censuses of returning fish). Panel B depicts median posterior estimates of the proportions-at-ocean age in the total spawning escapement (males plus females) by return year. Panel C shows the posterior estimates of the log abundance of each ocean age class in the spawning escapement by return year. Panel D depicts the estimated harvest rates for each ocean age class over time. For panels C and D, points and lines depict the median posterior estimates, and transparent boundaries indicate 95% credible intervals.

CHAPTER THREE. EFFECTS OF STOCHASTIC RECRUITMENT AND SELECTIVE HARVEST ON THE EVOLUTION AND MAINTENANCE OF ALTERNATIVE LIFE HISTORIES IN AGE-STRUCTURED POPULATIONS

3.1 ABSTRACT

Individuals within the same population may exhibit divergent approaches to achieving the same biological function. The maintenance of such life history polymorphisms is often explained using game theoretic concepts such as frequency-dependent selection. However, predictions from such models typically assume populations are at equilibrium. Among the most common examples of alternative phenotypes are those associated with reproduction. Alternative reproductive tactics are widespread in fishes, where they are often associated with variation in body size and age-at-maturity. However, fish populations also exhibit stochastic variability that is inconsistent with the assumptions of equilibrium population dynamics. It is possible then, that equilibrium expectations from eco-evolutionary models (*i.e.* frequency-dependent selection) may provide incomplete representations of the realized dynamics of alternative life histories in fishes. We explored how stochastic population dynamics interact with natural and sexual selection to shape the evolution and maintenance of alternative male phenotypes in Pacific salmon (*Oncorhynchus* spp.). Several species of Pacific salmon exhibit a mating system composed of typical 'hooknose' males that compete aggressively on the spawning grounds for mating opportunities after reaching a large body size at sea, and rarer 'jacks' that return from the ocean earlier at smaller sizes to attempt reproduction by 'sneaking'. Using a stochastic eco-evolutionary simulation model, we find that

levels of recruitment variation commonly observed in natural populations can increase the prevalence of jacks relative to equilibrium expectations. This result is largely attributable to the 'cohort mismatch' phenomenon, in which differences in age-at-maturity between male phenotypes can result in jacks from strong recruitment events maturing and spawning in the same year as hooknose males from weaker cohorts, elevating the prevalence of jacks in the breeding population. Simulation results were supported by long-term monitoring data which indicated a positive association between a stock's level of recruitment variation and its average jack prevalence in some (but not all) regions. Moreover, we find that frequency-dependent mating success can have important ramifications for how populations respond to harvest-induced selection. Our results emphasize that non-equilibrium population dynamics can be important to shaping the evolution and maintenance of alternative life histories.

3.2 INTRODUCTION

Understanding how multiple discrete life history pathways can co-exist within a population is an enduring puzzle in evolutionary ecology. Alternative phenotypes are widespread in animals, including structural polymorphisms (*e.g.* short versus long winged morphs in insects (Denno, Douglass, & Jacobs, 1986; Walker & Sivinski, 1986)), discrete resource use patterns (*e.g.* cannibalistic versus omnivorous individuals in amphibian populations (Pfennig, 1992; Pfennig & Collins, 1993)) and partial migration (*e.g.* residents versus migrants in fishes and birds (Chapman et al., 2012; Lundberg, 1988)). Reflecting discontinuous variation in one or more traits evolved towards the same function, the presence of such alternative phenotypes is inconsistent with classical evolutionary models in which a single optimal life history should exclude others through natural selection (Schaffer, 1997; Stearns, 1980). To resolve this apparent discrepancy, researchers often apply game theoretic principles to the study of life history evolution, such that an individual's fitness may vary based on the phenotypic expression of others in a population (Gross, 1984). A common example of such a mechanism is frequency-dependent selection (FDS), which occurs when the fitness of a given life history variant differs according to its relative abundance in the population (Ayala & Campbell, 1974; Heino, Metz, & Kaitala, 1998). By reducing the fitness of any tactic as it becomes more common, FDS can stabilize the coexistence of multiple alternative phenotypes within a population. Several other frameworks have been proposed as alternatives or complements to FDS (e.g. status-dependent selection; Gross, 1996; the environmental threshold model Heino, Metz, & Kaitala, 1998; Tomkins and Hazel 2007) yet predictions from each of these models implicitly assume a population that is at equilibrium, overlooking the fact that animal populations can vary stochastically across space and time. How population dynamics affect the evolution and maintenance of alternative life histories has been virtually unexplored in evolutionary biology (but see Clark & Yoshimura, 1993; Kisdi & Meszéna, 1993; Vincent & Brown, 1987), but may be important for understanding how harvesting and global change will affect species with such polymorphisms.

Among the most common examples of alternative phenotypes are those associated with reproduction. In species that experience intense sexual selection and variability in reproductive success, males may exhibit divergent approaches to achieving fertilizations, referred to as 'alternative reproductive tactics' (ARTs; Shuster & Wade, 2003; Taborsky, Oliveira, & Brockmann, 2008). A typical example of ARTs is the co-occurrence of males within a population that attempt to mate with females through territoriality, courtship, or monopolization of resources ('bourgeois males', *sensu* Taborsky, 1998), and those who try to gain fertilizations through sneaking or subterfuge ('parasitic males'). ARTs are particularly common in teleost fishes (Taborsky, 2008), where they are often associated with age-at-maturity and body size, and can influence a population's genetic diversity, age and size structure, and stock rebuilding potential (Hutchings & Rowe, 2008; Jones & Hutchings, 2002; Larsen et al., 2004; Hutchings, 2003). Amid growing recognition that the mating systems of exploited species should be considered in fisheries management (reviewed in Rowe & Hutchings, 2003), there has been substantial effort directed towards understanding the dynamics of ARTs in fish populations (reviewed in Taborsky, 2008). However, most fish stocks are also characterized by large and often unpredictable fluctuations in abundance and recruitment that severely violate the core assumptions of equilibrium population models (Hilborn & Walters 1992). Thus, equilibrium expectations of eco-evolutionary models may provide similarly incomplete or misleading descriptions of the realized dynamics of ARTs in fish populations. As such, understanding how population variability interacts with eco-evolutionary processes may be important for the management of exploited fish stocks, and offers insights into the evolution and maintenance of complex life histories under ecologically realistic scenarios.

Pacific salmon (*Oncorhynchus* spp.) are of economic, cultural, and nutritional importance to humans throughout their range from Eastern Russia and Japan to the west coast of North America. Several species of Pacific salmon exhibit a mating system composed of typical 'hooknose' males that compete aggressively on the spawning grounds for mating opportunities after reaching a large body size at sea, and rarer 'jacks', which migrate to the ocean but return to freshwater to spawn before the youngest females in a population (Quinn, 2005). While generally ineffective at acquiring mates through courtship and intrasexual contests due to their small body sizes, jacks possess numerous specializations for achieving fertilizations through 'sneaking', including a higher gonadosomatic index (Flannery, Butts, Słowińska, Ciereszko, & Pitcher, 2013), increased sperm velocity in river water (Flannery et al., 2013; Young, Conti, & Dean, 2013), and cryptic body coloration (Gross, 1984). Age-at-maturity in salmonids appears to be partially heritable (Carlson & Seamons, 2008) and sex-linked (Mckinney, Seeb, Pascal, Schindler, & Gilk-baumer, 2019) such that males sired by jacks are more likely to become jacks themselves (Heath, Rankin, Bryden, Heath, & Shrimpton, 2002). However, it is thought that all males are capable of maturing as jacks, contingent on reaching a critical growth or lipid accumulation threshold by a certain point in their juvenile development (Thorpe, 1986). As such, both environmental and genetic factors can shape a male's developmental 'decision' to become a jack (Heath, Rankin, Bryden, Heath, & Shrimpton, 2002; Vøllestad, Peterson, & Quinn, 2004). While there is evidence to suggest that alternative life histories of male salmon are maintained through FDS (Berejikian et al., 2010; Gross, 1984, 1985; Hutchings & Myers, 1994), several studies have questioned the feasibility of a stable evolutionary equilibrium in the presence of persistent stochastic variation in growth and survival (DeFilippo et al., 2019; Koseki & Fleming, 2006, 2007). Indeed, interannual variability in year-class strength combined with the difference in age-at-maturity between jack and hooknose males will necessarily affect the ratio of male phenotypes present in the breeding population (Koseki & Fleming, 2006; Koseki & Fleming, 2007). In such cases, jacks from strong recruitment events may mature and spawn in the same calendar year as hooknose males from weaker year-classes, leading to 'cohort mismatches' that elevate the relative abundance of jacks in the breeding population (DeFilippo et al., 2019). Such 'cohort mismatches' have been implicated in an increase of jacks in an introduced population of sockeye salmon (*O. nerka*) which has degraded local fishery yields and poses a difficult management challenge with no clear solution (DeFilippo et al. 2019).

Here, we investigate how stochastic population dynamics interact with natural and sexual selection and harvest to shape the evolution and maintenance of alternative male life histories. Using a stochastic individual-based eco-evolutionary simulation model that specifies interactions among environmental variation, demography, and reproductive behavior, we find that levels of recruitment variation commonly observed in natural populations can increase the prevalence of jacks in a population relative to equilibrium expectations. These simulation results were generally supported by long-term time-series of age composition and spawner-recruit data collected from natural salmon populations throughout North America, which indicated a positive relationship between a stock's level of recruitment variation and its average jack prevalence in some regions. Collectively, these findings demonstrate a novel role of population dynamics in the evolution and maintenance of alternative phenotypes and suggest that non-equilibrium dynamics may be more important in shaping the realized behavior of complex mating systems than is currently recognized.

3.3 METHODS

3.3.1 Simulation analysis

We developed an individual-based simulation model that incorporates interactions between genetics and life history traits (i.e. growth and maturation), as well as population-level ecological processes such as density-dependence and environmental variability (Fig. 3.1). Our approach is similar to existing eco-evolutionary models (e.g. Enberg, Jørgensen, Dunlop, Heino, & Dieckmann, 2009; Ohlberger, Schindler, Ward, Walsworth, & Essington, 2019), extended to represent the dynamics of alternative male mating phenotypes with frequency-dependent reproductive success, and parameterized to resemble a generic sockeye salmon (*O. nerka*) population. Individuals in this population spend two years in freshwater and can mature at ocean age-1 (total age (a) = 3), ocean age-2 ($a = 4$), or ocean age-3 ($a = 5$), the typical age classes found in sockeye salmon populations. Here, jacks are defined as males maturing at ocean age-1 and hooknose males are those maturing at either ocean age-2 or ocean age-3.

Annual recruitment to the population was specified in terms of the production of smolts (age-2 freshwater outmigrants) as a function of the number of sexually mature females in the breeding population ($N_F(t)$) according to a Beverton-Holt relationship (Fig. 3.1A):

$$N_{a=2,k,m=0}(t) = \frac{\alpha N_F(t-2)}{1+\beta N_F(t-2)} \mathrm{e}^{\xi_R(t-2)} \phi_k \tag{3.1}$$

$$\xi_R(t) \sim Normal(-0.5\sigma_R^2, \sigma_R^2)$$

where $N_{a=2,k,m=0}(t)$ is the number of age-2 smolts produced of sex k (where $k = 1$ represents females and $k = 2$ represents males). Here, the subscript m denotes maturity status, where $m = 0$ represents immaturity, and $m = 1$ represents sexual maturity. All individuals of age $a < 3$ are assumed to be immature. An adult-to-smolt stock-recruit relationship was chosen to integrate across the egg and juvenile stages in freshwater during which density-dependent mortality is greatest (Jonsson, Jonsson, & Hansen, 1998). In the Beverton-Holt function, α is the smolts per spawner at the limit of zero population size, β controls the degree of density dependence, and $\xi_R(t)$ are log-normally distributed recruitment deviations (Peterman, 1981) with a mean of 0, a variance of σ_R^2, and bias correction term $-0.5\sigma_R^2$. The number of recruits of a given sex ($x_{0,k}$) was calculated as the product of total recruits and a sex composition term (ϕ_k), which was fixed at 0.5.

Each individual (i) recruit inherits three quantitative genetic traits that, in conjunction with stochastic environmental effects, determine its life history trajectory: a growth rate coefficient (k) asymptotic adult size (L_∞), and an intercept of the probabilistic maturation reaction norm (γ_0) (PMRN; Dieckmann & Heino, 2007; Heino, Dieckmann, & Godø, 2002)). Given an individual's growth rate and asymptotic size, its length over time $L(i,t)$ follows a stochastic von Bertalanffy function (Fig. 3.1B):

$$L(i,t) = L(i,t-1) + k(i)(L_\infty(i) - L(i,t-1))e^{\xi_G(i,t)}$$

$$\xi_G(i,t) \sim N(-0.5\sigma_G^2, \sigma_G) \tag{3.2}$$

where, ξ_G is a log-normally distributed error term reflecting interannual variation in growth with a standard deviation of σ_G. The growth rate coefficient $k(i)$ here is equivalent to $1 - e^{-k'(i)}$

when k' is the Brody coefficient found in conventional parameterizations of the von Bertalanffy. Maturation was assumed to be a probabilistic function of individual length $L(i,t)$ and age $a(i,t)$ according to a linear PMRN with constant slope (λ) and width (σ_{PMRN}) (Fig. 3.1C):

$$p_{mat}(i,t) = 1/\left(1 + e^{-\left(\frac{(L(i,t)-\gamma_0(i))+\lambda a(i,t)}{\sigma_{PMRN}}\right)}\right) \tag{3.3}$$

where $\gamma_0(i) + \lambda a(i,t)$ is a linear function predicting the length at which the probability of maturation is 50% for age a. Individual maturation itself (m) is stochastic and determined through a Bernoulli trial with a probability of $p_{mat}(i,t)$. This specification of maturation is advantageous in that in reflects the joint influences of an individual's genetics $(k(i), L_\infty(i), \gamma_0(i))$ and environmental conditions (σ_G) on the maturation decision. Indeed, while maturing as a jack has been shown to be partially heritable (Hankin, Nicholas, & Downey, 1993; Heath et al., 2002), it is also environmentally influenced (Vøllestad et al., 2004), such that not all males sired by jacks will necessarily become jacks themselves, and a portion of males sired by hooknoses may mature as jacks. This variation is thought to be related to growth, where under favorable growing conditions, more juveniles are likely to mature as jacks, regardless of their genetic predisposition, and vice versa (Thorpe, 1986; Vøllestad et al., 2004).

Natural mortality was expressed through annual individual-level Bernoulli trials with an age-specific probability of survival s_a such that the number of individuals of each age $(a > 2)$ and sex alive at each time step ($N_{a>2,k}(t)$) was determined according to:

$$N_{a>2,k,m=0}(t) = \left(1 - P_{a,k}(t)\right)S_{a-1}(t)N_{a-1,k,m=0}(t-1) \tag{3.4}$$

where $N_{a-1,k,m=0}(t-1)$ is the number of immature individuals of the previous age class alive in the previous time step, and S_{a-1} is the proportion of individuals from the previous age class that survived natural mortality according to the individual-level Bernoulli trials with survival probability s_a. Similarly, $P_{a,k}(t)$ represents the proportion of individuals of a given age and sex reaching sexual maturity in year t according to the individual-level Bernoulli trials with maturation probabilities ($p_{mat}(i,t)$). The number of individuals of a given age and sex reaching maturity each year is then:

$$N_{a>2,k,m=1}(t) = P_{a,k}(t)S_{a-1}(t)N_{a-1,k,m=0}(t-1) \tag{3.5}$$

It should be noted that after participating in the year's breeding event, all mature individuals are removed from the population to represent the mortality associated with reproduction in semelparous species.

Of the females that reach sexual maturity each year, $N_F(t)$, the share of the subsequent recruits produced by each individual $f(i_{k=1})$ is hyperallometrically proportional to its length (Ohlberger et al., 2020a) relative to the total lengths of all females in the population $\sum_{i_{k=1,m=1,}=1}^{N_F(t)} L(i_{k=1,m=1,}, t)$:

$$f\left(i_{k=1,m=1,}, t\right) = \frac{L(i_{k=1,m=1,}, t)^{\varphi}}{\sum_{i_{k=1,m=1,}=1}^{N_F(t)} L(i_{k=1,m=1,}, t)^{\varphi}} N_{a=2,}(t+2) \tag{3.6}$$

where $N_{a=2,}(t+2)$ is the total number of recruits produced by the year t breeding event according to Beverton-Holt adult-to-smolt recruitment and φ is the fecundity exponent that was fixed at $\varphi = 1.8$. Ohlberger et al. (2020b) estimated that length and fecundity are related allometrically with an exponent of 2.36 for Chinook salmon (*O. tshawytscha*), which leads to an age composition skewed towards older, larger age classes, as is observed in this species. Reducing this value to 1.8 produced an age and size distribution more typical of sockeye salmon (Appendix C, Fig. C7). The actual number of smolts produced by each female was multinomially distributed, with a set of probabilities equal to the fecundities of all females in the breeding population $f(i)$, and a number of trials equal to the total number of recruits ($N_{a=2}(t+2)$)

Each female probabilistically selects a male to sire her offspring. Mating was non-assortative with respect to age, body size, or genotype. For jack males, the chance of mating was solely dependent on the prevalence of jacks in the breeding population, according to a linear frequency-dependent mating function (Fig. 3.1G):

$$\frac{\delta_J(t)}{\delta_H(t)} = \begin{cases} \mu(1-\theta_{FDS}) + \theta_{FDS}\left(\frac{N_J(t)}{N_H(t)}\right) & , N_J(t) > 0 \\ 0 & , N_J(t) = 0 \end{cases} \tag{3.7}$$

where:

$$N_J(t) = N_{a=3,k=2,m=1}(t) \tag{3.8}$$

and

$$N_H(t) = \sum_{a=4}^{5} N_{a,k=2,m=1}(t) \tag{3.9}$$

Here, $\frac{\delta_J(t)}{\delta_H(t)}$ is the ratio of eggs sired by jack males ($\delta_J(t)$) relative to hooknose males ($\delta_H(t)$), which is a function of the ratio of jacks ($N_J(t)$) to hooknose males ($N_H(t)$) present on the spawning grounds, the strength of negatively frequency-dependent mating success (θ_{FDS}), and μ, which is the jack:hooknose ratio at which the ratio of eggs fertilized by each male variant is equal to the ratio in which they are present (i.e. where the frequency-dependent function crosses the 1:l line).

The proportion of a given cohort sired by jacks $\psi_{w=2}(t)$ is then calculated as:

$$\psi(t) = \frac{\frac{\delta_J(t)}{\delta_H(t)}}{\frac{\delta_J(t)}{\delta_H(t)} + 1} = \frac{\delta_J(t)}{\delta_J(t) + \delta_H(t)}. \tag{3.10}$$

Here, for each individual jack, its probability of siring a female's offspring ($\pi\left(i_{a=1,k=2,m=1}, t\right)$) is equal to the total proportion of offspring sired by jacks that year ($\psi(t)$) relative the total number of jacks present:

$$\pi\left(i_{a=3,k=2,m=1}, t\right) = \frac{\psi(t)}{N_J(t)} \tag{3.11}$$

Similarly, for hooknose males, an individual's probability of mating depends on the total proportion of offspring sired by hooknose males according to the frequency-dependent mating function ($1 - \psi(t)$). To reflect the reproductive advantage of large body size for hooknose males with respect to intrasexual competition and female mate choice, an individual hooknose male's probability of mating ($\pi\left(i_{a>3,k=2,m=1}, t\right)$) was also directly proportional to its relative length:

$$\pi\left(i_{a>3,k=2,m=1}, t\right) = \frac{1-\psi(t)}{N_H(t)} \frac{L(i_{a>3,k=2,m=1}, t)}{\sum_{i_{a>3,k=2,m=1}=1}^{N_H(t)} L(i_{a>3,k=2,m=1}, t)} \tag{3.12}$$

Reproductive output is thought to depend less heavily on body size for males than for females (Quinn, 2005), hence the direct rather than exponential relationship here. Size and age-at-maturity are often assumed to be polygenic quantitative traits controlled by many loci (Conner & Hartl, 2004). However, there is a growing body of evidence that these characteristics (Barson et al., 2015; McKinney, Seeb, Pascal, Schindler, & Gilk-Baumer, 2019) and male reproductive tactics specifically (Heath et al. 2002) follow sex-linked inheritance in salmon. As a simplified representation of this mode of inheritance, males and females inherit trait values from their father and mother respectively rather than a mix of both parents in the model. For simplicity, it is assumed that the primary trait passed down to an individual's offspring is the intercept of the PMRN (γ_0):

$$\gamma_0(\mathrm{o}_k) \sim Normal\left(\gamma_0(i_k), \vartheta\gamma_0^{ref}\right) \tag{3.13}$$

where $\gamma_0(\mathrm{o}_k)$ represents the trait value of an offspring of sex k, $\gamma_0(i_k)$ is the trait value of the offspring's same-sex parent, γ_0^{ref} is the reference value for the intercept of the PMRN and ϑ is a coefficient of variation for the PMRN intercept that represents a time-invariant mutation-recombination-segregation kernel, implying constant genetic variance (Enberg et al., 2009). The evolutionary dynamics are assumed to be driven by the intercept of the PMRN, with trait values changing in response to natural and sexual selection. We chose to model trait changes in the reaction norm intercept because available evidence suggests that evolution is more likely to shift the intercept rather than the slope of the PMRN (Eikeset et al., 2016)

Values for the offspring's growth parameters were then specified based on fixed genetic correlations with the intercept of the PMRN. We assumed a positive correlation between asymptotic size and the intercept of the PMRN (ρ_{γ_0,L_∞}), such that that individuals disposed to mature early (smaller intercept of the PMRN) will be more likely to achieve a smaller final body size (Fig. 3.1E):

$$L_\infty(i) = L_\infty^{ref} + \rho_{L_\infty,\gamma_0}\left(\gamma_0(i) - \gamma_0^{ref}\right) \tag{3.14}$$

Similarly, we assumed that an individual's growth rate and asymptotic size are negatively correlated ($\rho_{L_\infty,k}$, Fig. 3.1D), based on results from fisheries stock assessments (Pacific Fishery Management Council 2008; Helser, Stewart, & Lai, 2007):

$$k(i) = k^{ref} + \rho_{L_\infty,k}\left(L_\infty(i) - L_\infty^{ref}\right) \tag{3.15}$$

where k^{ref}, and L_∞^{ref} are the reference values for growth rate and asymptotic size respectively. As such, individuals that grow more slowly are expected to take longer to mature and reach a larger asymptotic size.

In addition to the base simulation model described above, we also explored the effect of harvest on the population with varying degrees of fishing mortality and size-selectivity. In the harvest sub-model, a target exploitation rate (u^{target}) was defined to determine the fully selected fishing mortality in a given year (F_t^{target}):

$$F_t^{target} = -log(1 - u^{target}) \tag{3.16}$$

Each sexually mature individual then exhibits a probability of being harvested $p_{catch}(i)$ that is determined by the target fishing mortality in that year and the individual's body size:

$$p_{catch}(i_{m=1}, t) = 1 - \mathrm{e}^{-F_t^{target} v(i_{m=1})} \tag{3.17}$$

where $v(i)$ represents the vulnerability of an individual to harvest according to the function:

$$v(i_{m=1}) = e^{\frac{-\left(\log\left(L(i_{m=1},t)\right) - \log(L_{max})\right)^2}{2\sigma_{catch}^2}} \tag{3.18}$$

which forms a dome-shaped selectivity curve where L_{max} is the length at which an individual's vulnerability to harvest is maximized at 1, and σ_{catch} determines the width of the curve (Fig. 3.1F). L_{max} was positioned to create an asymmetrical dome-shaped selectivity curve characteristic of salmon gillnets where the smallest individuals are less vulnerable than the largest (Bromaghin, 2005). Whether or not an individual is harvested (H) is then determined through a Bernoulli trial with a probability of $p_{catch}(i)$. Because the realized exploitation rate (u^{real}) may differ from the fully selected harvest rate depending on the assumed selectivity curve relative to the size structure of the population, the realized exploitation rate was then calculated as the total number of individuals harvested divided by the total number of individuals that return (mature) in any given year ($N_R(t)$) :

$$u^{real} = \frac{\sum_{i=1}^{N_R(t)} Bernoulli(p_{catch}(i_{m=1}, t))}{N_R(t)} \tag{3.19}$$

Where:

$$N_R(t) = \sum_{a=3}^{5} \sum_{k=1}^{2} N_{a,k,m=1}(t) \tag{3.20}$$

3.3.2 Model simulations

Individuals were monitored for age (a), length (L), trait values ($k(i), L_\infty(i), \gamma_0(i)$) and maturity status (mature or immature). In the first year of a simulation, the number of recruits was defined using the asymptotic smolt recruitment (α/β), and PMRN intercept values of all individuals were randomly drawn from a normal distribution with mean γ_0^{ref} and a broad standard deviation of 200. In each year of the simulation, individual sizes were calculated using the von Bertalanffy growth function, and the maturation reaction norm was applied to specify the number of mature fish. In the first year of the simulation, the age and size structure was initiated by projecting the asymptotic smolt recruitment through each age class and applying the growth function and survival and maturation probabilities (Appendix C, Supplementary Methods). In subsequent years, the number of mature individuals was used as the spawner abundance to determine adult-to-smolt recruitment. Recruits enter the population as immature fish, assuming an initial size of 30mm at $a = 1$, and each year, individuals that survive grow and transition into the next age class, or mature and join the breeding population before dying.

Reference values for the parameters for all equations were specified based on values from published literature where available (Table C1). While the simulation model was parameterized to resemble a sockeye salmon population, parameter values from similar species or analyses were used when necessary. For parameters with no published or intuitive estimates, values were selected by tuning the simulation model to generate values for emergent quantities, such as the population age composition and size-at-age, that resembled those observed in empirical data from sockeye salmon populations (Appendix C, Fig. C6, C7). Initial values for all generated quantities within the model were calculated by running the simulations for 100 years with stochastic growth and recruitment terms set to 0 (Appendix C, Fig. C5). Stochastic simulations were then run for 400 years, with the first 200 years treated as an additional 'burn in' period. Population dynamics were simulated over a range of values for recruitment variability ($\sigma_R = 0.0 - 1.0$; Thorson, Jensen, & Zipkin, 2014; Wilson White, Botsford, Hastings, & Holland, 2014) as well as variation in growth (σ_G= 0.1-0.3; Ohlberger, Schindler, Ward, Walsworth, & Essington, 2019; Wilson White et al., 2014). Additionally, frequency-dependent mating success (θ_{FDS}) was simulated across a range of values from $0.1 - 0.9$, where higher values reflect weaker negative frequency-dependence (a value of 1 indicates no frequency-dependence, Fig. 3.1G), and we explored scenarios across a range of equilibrium mating frequencies (μ, the jack:hooknose ratio at which the relative reproductive success of each phenotype is equal to the ratio in which they are present; $\mu = 0.$ 0.0001, 0.01, 0.05). For scenarios in which harvest occurred, we explored target exploitation rates from 0.1 to 0.6, with selectivity ranging from narrowly size-selective to completely unselective (Fig. 3.1F). In all simulations, we monitored the prevalence of ocean age-1 males (jacks) within cohorts (by brood year), and in the breeding population prior to harvest (by return year). The prevalence of females maturing at ocean age-1 (‘jills’) was fixed at 0.01 to reflect the rarity of these individuals in natural salmon populations (Quinn, 2005). All simulations were coded and run using the R statistical computing environment (R Core Team, 2015).

3.3.3 Empirical analysis

Using long-term time-series of spawner-recruit and age composition data for natural sockeye salmon populations throughout North America, we evaluated the relationship between the prevalence of jacks in each population relative to its variability in recruitment. We fit the following Bayesian hierarchical Ricker stock-recruit model (Ricker, 1954) using long-term data (27-62 years for each population) on sockeye salmon populations from the Fraser River in British Columbia (17 stocks), Bristol Bay (7 stocks), and the Westward region (Alaska Peninsula and Kodiak Archipelago) (8 stocks) of Alaska (Table C2):

$$\log\left(R_{p,y}\right) = \log\left(S_{p,y}\right) + \log\left(\alpha_p\right) - \beta_p S_{p,y} + \phi\omega_{p,y-1} + \varepsilon_{p,y} \qquad (3.21)$$

where α_p and β_p are the productivity and (inverse) capacity terms for population p, and $R_{p,y}$ are the number of adult recruits to population p and brood year y that resulted from the escapement in that year ($S_{p,y}$). We assumed that the form of recruitment variation likely to trigger cohort mismatches would be ‘white noise’ rather than autocorrelated deviations associated with low-frequency fluctuations in productivity (Peterman & Dorner, 2012). As such, we decomposed the deviations from the stock-recruit relationship into autocorrelated and independent error components (Fleischman, Catalano, Clark, Bernard, & Chen, 2013) where ϕ is the AR lag-1 coefficient of the previous year’s model residual $\omega_{p,y}$ such that:

$$\omega_{p,y} = Log(R_{p,y}) - \log(S_{p,y}) - \log(\alpha_p) + \beta_p S_{p,y} = \phi\omega_{p,y-1} + \varepsilon_{p,y} \tag{3.22}$$

and $\varepsilon_{p,y}$ are the independent normally distributed recruitment deviations:

$$\varepsilon_{p,y} \sim Normal\left(0, \sigma_{R_p}\right) \tag{3.23}$$

While the Ricker function is standard for analyzing sockeye salmon stock-recruit data, we also repeated the analysis described here assuming a Beverton-Holt spawner recruit function (Appendix C, Fig. C8). Productivity parameters were modelled hierarchically as random variables arising from a common distribution that was shared among populations:

$$\log(\alpha_p) = \mu_\alpha + \sigma_\alpha z_{a_p} \tag{3.24}$$

where μ_α is the among-population mean productivity and σ_α is the standard deviation. To improve posterior sampling efficiency and mitigate the bias that can result from estimating hierarchical models using Monte Carlo methods (Betancourt, 2016; Monnahan, Thorson, & Branch, 2017), a non-centered parameterization was used, where z_{a_p} is a standard scaling factor for each population that follows a normal distribution with a mean of zero and a standard deviation of one (Monnahan et al., 2017). The mean of the distribution of log productivity (μ_α) was drawn from a vague normal prior distribution with a mean of 0 and a standard deviation of 20, and σ_α was drawn from a Cauchy distribution with location of 0 and scale of 2.5. Because the capacity terms (β_p) are not transportable between populations (Hilborn & Liermann, 1998), these parameters were specified independently for each stock with a normal prior distribution of mean zero and standard deviation of 1.

The recruitment variation terms (σ_{R_p}) were also modelled hierarchically among populations using a non-centered approach:

$$\log\left(\sigma_{R_p}\right) = \mu_{\sigma_R} + \sigma_{\sigma_R} z_{\sigma_{R_p}} \tag{3.25}$$

where μ_{σ_R} and σ_{σ_R} were both drawn from Cauchy prior distributions with locations of 0 and scales of 2.5. The estimated recruitment variation term for each population (σ_{R_p}) was then related to its jack prevalence according to:

$$p_{p,y}^{J} = L_p \tag{3.26}$$

$$L_p \sim Normal\left(\mu_L, \sigma_{L_r}\right) \tag{3.27}$$

$$\mu_L = \mu_{r(p)} + \tau_{r(p)}\, \sigma_{R_p} \tag{3.28}$$

where $p_{p,y}^{J}$ is the estimated logit proportion jacks in population p in year y, and L_i is a random effect describing that population's jack prevalence with a mean μ_L defined by a linear function with region-specific (e.g. Bristol Bay, Fraser, Westward AK) intercept $\mu_{r(p)}$ and slope $\tau_{r(p)}$, and residual population-level variation in jack prevalence σ_{L_r}. All standard deviation terms were drawn from Cauchy prior distributions lower-bounded at zero with a location term of zero and scale of 2.5. Spawner abundance ($S_{p,y}$) was assumed to be observed without error and recruits were assumed to follow a lognormal likelihood:

$$R_{p,y}^{obs} \sim Lognormal\left(\log\left(R_{p,y}\right), \sigma_{recruits}^{obs}\right) \tag{3.30}$$

where $R_{p,y}^{obs}$ are the observed adult recruits for population p and year y and $\sigma_{recruits}^{obs}$ is the lognormal observation error term for these data which was fixed at 0.5. The observed logit jack proportions ($\text{logit}(p_{p,y}^{J_{obs}})$) were assumed to be normally distributed around the estimated values $p_{p,y}^{J}$with region specific observation error terms ($\sigma_{r(p)}^{J_{obs}}$) which were freely estimated:

$$logit\left(p_{p,y}^{J_{obs}}\right) \sim Normal\left(p_{p,y}^{J}, \sigma_{r(p)}^{J_{obs}}\right) \tag{3.31}$$

We excluded the Nushagak River (Bristol Bay) and Harrison Lake (Fraser River) populations as both of these exhibit a freshwater age-0 life history that likely affects the prevalence of jacks in these populations. Posterior sampling occurred in stan (Stan Development Team, 2015), implemented in R via the Rstan package (Gelman, 2014).

3.4 RESULTS

3.4.1 Demographic simulation

The prevalence of jacks within the population was highly variable across the dimensions of both frequency-dependence (θ_{FDS}), and recruitment variation (σ_R). When negative frequency-dependent mating success was strongest (i.e. θ_{FDS} = 0-0.2), jacks were maintained in the population at low levels (~5% of males, Fig. 3.2). Conversely, when the strength of negative frequency-dependent mating was relaxed (i.e. θ_{FDS} = 0.7-0.9), as much as 50-100% of males in the population matured as jacks (Appendix C, Fig. C1).

At all values of frequency-dependence that did not result in a majority of males maturing as jacks at equilibrium (θ_{FDS} = 0-0.6), the jack prevalence of the population increased with greater recruitment variation (Fig. 3.2). For instance, at θ_{FDS} = 0.5, the equilibrium proportion of males maturing as jacks within cohorts was 0.11, which increased to 0.14 at σ_r=0.3, 0.17 at σ_R=0.6, and reached 0.21 at σ_R=1.0, an increase of over 80% (Fig. 3.2A). Recruitment variation had a much larger effect on the prevalence of jacks in the breeding population, elevating it by over 130% in certain parameter regions (Fig. 3.2B). This is not surprising as the prevalence of jacks in the breeding population effectively represents the influence of recruitment variation and 'cohort mismatching' before any dampening influence of frequency-dependent mating is introduced.

The effect of recruitment variation on the maintenance of jacks in in the population was not consistent across levels of frequency-dependence. For instance, when θ_{FDS} was relaxed such that ≥50% of males in the population matured as jacks (β_{FDS} = 0.7-0.9), increasing recruitment variation actually decreased the levels of jacks in the population (Appendix C, Fig. C1). At the strongest levels of frequency-dependence β_{FDS} = 0-0.2, recruitment variation increased the proportion of individuals maturing as jacks, but the effect was smaller than at intermediate levels (β_{FDS} =0.3-0.5) (Fig. 3.2). The assumed equilibrium jack:hooknose mating frequency (μ) had a substantial positive effect on the prevalence of jacks in the population, but dampened the relative effect of recruitment variation on increasing jack proportions (Appendix C, Fig. C2, C3). By contrast, growth variation had little impact on the level of jacks in the population (Appendix C, Fig. C2, C3).

3.4.2 Harvest simulations

Fishing had little effect on the proportion of individuals maturing as jacks in the population when vulnerability to harvest was unrelated to body size, even at high levels of fully selected fishing mortality (Fig. 3.3). Conversely, when harvest was size-selective for larger individuals, fishing could increase jack prevalence substantially compared to an unfished population in the same parameter space (Fig. 3.3). However, the effects of size-selective harvest were largely dependent on the degree of frequency-dependent mating that was assumed. When mating success was strongly frequency-dependent, harvest had little effect on the prevalence of jacks in the population, regardless of fishing mortality or size selectivity (Fig. 3.3 all panels). Alternatively, when frequency-dependent mating was relaxed ($\theta_{FDS} = 0.5$) size-selective fishing could increase jack proportions substantially, producing scenarios in which jacks became the dominant male life history. There was little evidence to suggest that recruitment variation and size-selective harvest interacted synergistically. Indeed, for most levels of frequency-dependence, fishing mortality, and size-selectivity, the effects of harvest were similar across the three levels of recruitment variation that we explored. However, for $\theta_{FDS} = 0.5$, increasing recruitment variation acted to dampen the effects of high fishing mortality and selectivity, preventing extreme increases in jack prevalence (compare Fig. 3.3A to Fig. 3.3C). For instance, at σ_R = 0.4, strongly size-selective high exploitation rates increased the jack proportion by up to almost 0.7 (Fig. 3.3A) while this increase was reduced to less than 0.4 when σ_R was higher (Fig. 3.3C).

3.4.3 Empirical results

Estimated posterior distributions for coefficients relating a population's average jack prevalence to its level of recruitment variability were mostly positive for the Westward Alaska stocks (b_1, median= 3.52, 95% credible interval = 0.14, 7.48) and Fraser River stocks (b_2, median= 1.54, 95% credible interval = -1.43, 4.47), but not for Bristol Bay populations (b_3, median= -0.93, 95% credible interval = -6.48, 4.9) (Fig. 3.4). In the Westward Alaska region, the population with the most variable recruitment (median $\sigma_R = 0.62, 95\%$ credible interval $= 0.5, 0.84$) and highest jack prevalence (median=0.06, 95% credible interval = 0.04, 0.08) was Frazer Lake on Kodiak Island, while the Black Lake (median $\sigma_R = 0.24, 95\%$ credible interval $= 0.12, 0.40$) and Chignik Lake (median $\sigma_R = 0.25, 95\%$ credible interval $= 0.15, 0.36$) populations of the Alaska Peninsula exhibited the most stable recruitment dynamics and lowest jack proportions (Black Lake median = 0.0008, 95% credible interval = 0.0006, 0.0011, Chignik Lake median = 0.0027, 95% credible interval = 0.002, 0.004). Among the Fraser River populations, the most variable were the Late Stuart (median $\sigma_R = 1.1, 95\%$ credible interval $= 0.88, 1.36$) and Portage (median $\sigma_R = 1.02, 95\%$ credible interval $= 0.82, 1.29$) populations while the Birkenhead (median= 0.022, 95% credible interval=0.014, 0.034) and Gates (median= 0.049, 95% credible interval=0.029, 0.081) stocks exhibited the highest jack prevalence with less extreme (but still substantial) recruitment variation (median $\sigma_R = 0.67, 0.78$ respectively). Populations in the Bristol Bay region exhibited by far the lowest jack proportions, with no population exceeding a median estimated jack prevalence of 0.003, despite several populations with substantial recruitment variation (e.g. Alagnak, Kvichak, Ugashik, Igushik, median $\sigma_R = \sim 0.50$).

3.5 DISCUSSION

Our simulation results demonstrate that recruitment variation can have a pronounced effect on the prevalence of jacks in a population. The mechanism behind this increase appears to be similar to the 'cohort mismatch' phenomenon reported previously in a single sockeye salmon stock from Frazer Lake on Kodiak Island (DeFilippo et al. 2019). Briefly, cohort mismatches can occur in age-structured populations where individuals maturing at different ages in the same calendar year are the products of different recruitment events. Therefore, if recruitment is variable and largely determined early in life (*i.e.* freshwater and early marine residency), the age composition of the spawning population will not be representative of the actual maturity schedule within year classes, but will reflect the relative abundance of the different cohorts from which each age class originates as well. Consequently, jacks from strong recruitment events may frequently reach maturity and spawn in the same year as older individuals from weaker recruitment events that occurred in previous years. In this scenario, even if jacks are only a small percentage of each cohort, they may nonetheless comprise a large proportion of the breeding population in a given year and subsequently fertilize a large share of the eggs. While negative frequency-dependent mating will reduce the average reproductive success of jacks in such events, the total fertilizations obtained by jacks collectively may still be higher than in years when jacks are rare (Ayala & Campbell, 1974, Fig. 3.1G). If the jack life history is heritable, this will cause an elevated proportion of the ensuing cohort to be predisposed to mature as jacks as well. This mechanism was implicated in the increasing prevalence of jacks in Frazer Lake sockeye salmon over the last few decades, and our simulation results demonstrate that recruitment variation can override the stabilizing influence of frequency-dependent selection in certain circumstances. Importantly, our results show that cohort mismatches serve to increase the prevalence of a given life history only when it is not dominant (<50%). As such, it is possible that the results described here with regards to alternative male phenotypes are actually a special case of a broader phenomenon in which recruitment variability promotes greater evenness in the maturation schedules of age-structured populations. Indeed, in the absence of frequency-dependent selection, recruitment variation and cohort mismatching could exert an even stronger effect on homogenizing the age distribution, assuming a heritable component to age-at-maturity. It should be noted that we estimated an average white noise recruitment variation term (σ_R) of 0.52 (95% credible interval = 0.42, 0.61) for the sockeye populations examined here, well within the range of values at which jack proportions were observed to increase in our simulations.

In addition to recruitment variation, our simulation showed that fisheries can amplify the prevalence of jacks in a population, but only when harvest was size-selective. This result is not surprising, as any increase in the mortality cost incurred by the hooknose life history would be expected to lead to an evolutionary response favoring a higher equilibrium jack frequency in the population (Gross, 1991). More broadly, several previous studies have shown evidence for harvest-induced shifts in population size and age structure (Hutchings, 2005; Kendall, Dieckmann, Heino, Punt, & Quinn, 2014; Swain, Sinclair, & Hanson, 2007). However, few studies have examined the effects of fishing on traits that are under complex patterns of selection such as frequency-dependence. We found that size-selective harvest only induced a substantial evolutionary shift when frequency dependent selection was moderate or relaxed (Fig. 3.3), with virtually no evolutionary response when FDS was strongest. This result emphasizes that frequency-dependent mating success and sexual selection can filter how populations respond to fisheries-induced selection (Hutchings & Rowe, 2008; Weir, Kindsvater, Young, & Reynolds, 2016).

In salmon, jacks experience a survival advantage over hooknose males due to their shortened marine residency, but are also subject to frequency-dependent reproductive success on the spawning grounds. While any increased mortality on hooknose males should increase the relative mean fitness of jacks —and by extension their prevalence in the population— this may not necessarily occur as expected if FDS is an important control of male fitness. For instance, increased mortality of hooknose males would lead to a direct increase in the prevalence of jacks on the spawning grounds, but the number of fertilizations actually achieved by jacks will not increase proportionally due to FDS, mediating the population's realized evolutionary response to harvest. The magnitude of this discrepancy likely depends on the strength of FDS, and the relative importance of survival versus mating success as components of male fitness functions. The role of FDS in dampening a population's evolutionary response to harvest may explain why documented increases in the prevalence of jacks in exploited salmon populations are not common despite long histories of size-selective fisheries and wide availability of long-term monitoring data (but see DeFilippo et al., 2019; Young, Cluney, & Weir 2020). Recruitment variation did not interact substantially with the effects of size-selective harvest except to dampen the occurrence of extreme evolutionary shifts (*i.e.* towards the majority of males maturing as jacks) associated with intense size selective harvest and relaxed frequency dependence. This is likely due to the fact that recruitment variation acts to homogenize the age distribution relative to equilibrium expectations, while harvest acts to increase the equilibrium frequency of jacks.

The spawner-recruit and age composition data analyzed here generally indicated a positive relationship between a stock's level of recruitment variation and its average jack prevalence, suggesting that population dynamics may be a salient factor in maintenance of alternative life histories across salmon populations. However, the evidence for this correlation is equivocal, and there was no support for a positive relationship between recruitment variation and jack prevalence among Bristol Bay stocks. There are several reasons why such a relationship may not be discernable in this region. For instance, each Bristol Bay stock considered here is defined at the river scale, and is actually composed of dozens of distinct individual spawning populations (Hilborn, Quinn, Schindler, & Rogers, 2003). Bristol Bay sockeye salmon are known for their extensive biocomplexity and the stabilizing effect that this population diversity exerts on their aggregate dynamics (Schindler et al., 2010; White, Botsford, Hastings, & Holland, 2014). As such, recruitment variation measured at the river scale is an underestimate of the realized variability within individual spawning units. While the other Alaskan stocks considered here and those of the Fraser River are also composites of multiple subpopulations, their biocomplexity is not as extensive as that of Bristol Bay (Griffiths et al., 2014). Additionally, enumeration of jacks may be more difficult for the Bristol Bay stocks compared to other regions. Indeed, abundance and age composition are estimated using weirs at all of the Westward Alaskan populations, which presumably have near perfect accuracy for detecting jacks. Conversely, age composition for Bristol Bay stocks is determined by beach seining, which likely has coarser resolution for detecting the smaller and rarer jacks. This explanation is consistent with the generally low jack proportions and lack of contrast among Bristol Bay stocks (Fig. 3.4E). Moreover, a strong genetic basis for the jack life history is a necessary facet for the ‘cohort mismatch’ phenomenon to affect the jack prevalence of a population. While understanding of the genetics underlying age-at-maturity in salmon is still incomplete, there is evidence that the genetic architecture can vary between populations (McKinney et al., 2019). As such, it is possible that the genetic basis of age-at-maturity may be weaker in Bristol Bay sockeye, such that these populations may not be as vulnerable to experiencing increases in jack proportions via cohort mismatches. Finally, there may simply be other mechanisms not accounted for in our analysis such as exploitation history (i.e. harvest intensity and size-selectivity) or habitat conditions in spawning locations (e.g. DeFilippo et al., 2018) which are more important in shaping the dynamics of alternative life histories in Bristol Bay sockeye salmon.

From a management standpoint, an increase in the prevalence of small-bodied, early maturing phenotypes is not desirable, as such individuals are typically of little value to recreational and commercial fisheries. In areas where jacks have increased to high levels, local fishing fleets have seen declines in realized yield owing to the reduced marketability of jacks to processors and retailers (Foster & Schaberg, 2016). Concerns of increasing jack prevalence in exploited salmon populations typically assume a direct mechanism of size-selective harvest, whereby increased removals of older males leads to an evolutionary shift in favor of jacks (Gross, 1991). While our results do indicate that size-selective harvest can substantially elevate the prevalence of jacks in a population, we also find that non-trivial increases can be achieved by recruitment variation alone. Thus, any factors that induce population variability may also be associated with rising jack proportions. Increasing variability in fish populations can arise from natural environmental shifts that alter recruitment and survival rates (Kilduff, Di Lorenzo, Botsford, & Teo, 2015), as well as anthropogenic activities such as erosion of biocomplexity within (*i.e.* age and life history diversity) and among spawning units (*i.e.* multiple incoherent population components) (Carlson & Satterthwaite, 2011; Moore, Mcclure, Rogers, & Schindler, 2010). Moreover, several studies have indicated that intense exploitation rates can amplify population variability, providing a possible mechanism by which harvest could induce cohort mismatches as well (Anderson et al., 2008; Essington et al., 2015; Hsieh et al., 2006). As such, managers concerned with unwanted shifts in the age composition of an exploited stock may need to consider a broader range of potential mechanisms beyond direct size selective fishery removals. However, the effects of recruitment variation on jack proportions were still relatively small compared to the potential increases due to size-selective harvest, and controlling selectivity is likely to be a much more tractable management option than stabilizing population dynamics. Importantly, our harvest simulations showed that a population's evolutionary response to selective harvest can be heavily influenced by the strength of FDS, suggesting that empirical measurements of frequency-dependent mating success (e.g. Berejikian et al., 2010) may be particularly useful for predicting how the frequencies of alternative male life histories will respond to fishing, environmental change, and alternative management strategies (Gross, 1991).

Substantial uncertainty in parameter values (only a limited dimension of which was explored here), functional forms assumed (*e.g.* alternative forms of frequency-dependent selection), and the influences of additional ecological processes not considered here (*e.g.* interspecific interactions, fine-scale habitat conditions, behavioral plasticity) may interact with or modulate the effects of recruitment variation and harvest on the maintenance of alternative life histories beyond what our simulations account for. Moreover, the genetics of age-at-maturity in our model was a simplification of what appears to be a far more complex and variable system of inheritance (McKinney et al 2019), and previous studies have shown that the genetic architecture of a trait can have important effects on how it will respond to selection (Kuparinen & Hutchings, 2017; Oomen, Kuparinen, & Hutchings, 2020). We present these results as a heuristic demonstration of how population dynamics and harvest could reshape the maintenance of alternative life histories in fish populations. While the empirical results presented here, and those of previous studies (DeFilippo et al. 2019) indicate that the phenomena presented in our simulations may occur in at least some cases, any specific predictions or prescriptions for individual populations should be based on simulation studies more carefully parameterized to reflect their specific demographic and genetic conditions.

As evidence accumulates that evolution can occur over contemporary time scales, understanding how evolutionary and ecological processes interact becomes increasingly important to predicting the realized behavior of natural populations (Stockwell, Hendry, & Kinnison, 2003). Here, we demonstrate that recruitment variation can interact with natural and sexual selection to produce emergent dynamics that could not be predicted from purely evolutionary models. These results underscore the need for models of ARTs to carefully consider the ecological context in which the adaptive dynamics are playing out (*e.g.* Eadie & Fryxell, 1992). ARTs appear particularly common in fishes (Oliveira, Taborsky, & Brockmann, 2008), and most fish populations are also characterized by persistent demographic variability (Smith, 1994; Thorson et al., 2014). As such, models of ARTs in fishes should consider the effects of non-equilibrium population dynamics on the maintenance of alternative phenotypes (Vincent & Brown, 1987). To the extent that ARTs can affect the management of commercially valuable fish stocks (DeFilippo et al., 2019; Hutchings & Myers, 1988; Larsen et al., 2004; Rowe & Hutchings, 2003), predicting their responses to environmental change or alternative harvest strategies may be important considerations for fisheries. Future studies should explore the effects of fishing and population variability on the maintenance of ARTs in other taxa with different life histories (e.g. iteroparous species, more complex age structure), as well as the effects of different frequencies of variation (Bjørnstad, Nisbet, & Fromentin, 2004; Wilson White et al., 2014; Worden, Botsford, Hastings, & Holland, 2010), and the potential outcomes of different harvest and management strategies. In particular, closed loop simulations that specify some of the mechanisms identified here using empirically estimated parameter values will likely be especially useful for evaluating the effects of alternative harvest and management strategies (e.g. Management Strategy Evaluation; Punt, Butterworth, de Moor, De Oliveira, & Haddon, 2016) on the frequencies of alternative male phenotypes in exploited populations.

3.6 FIGURES

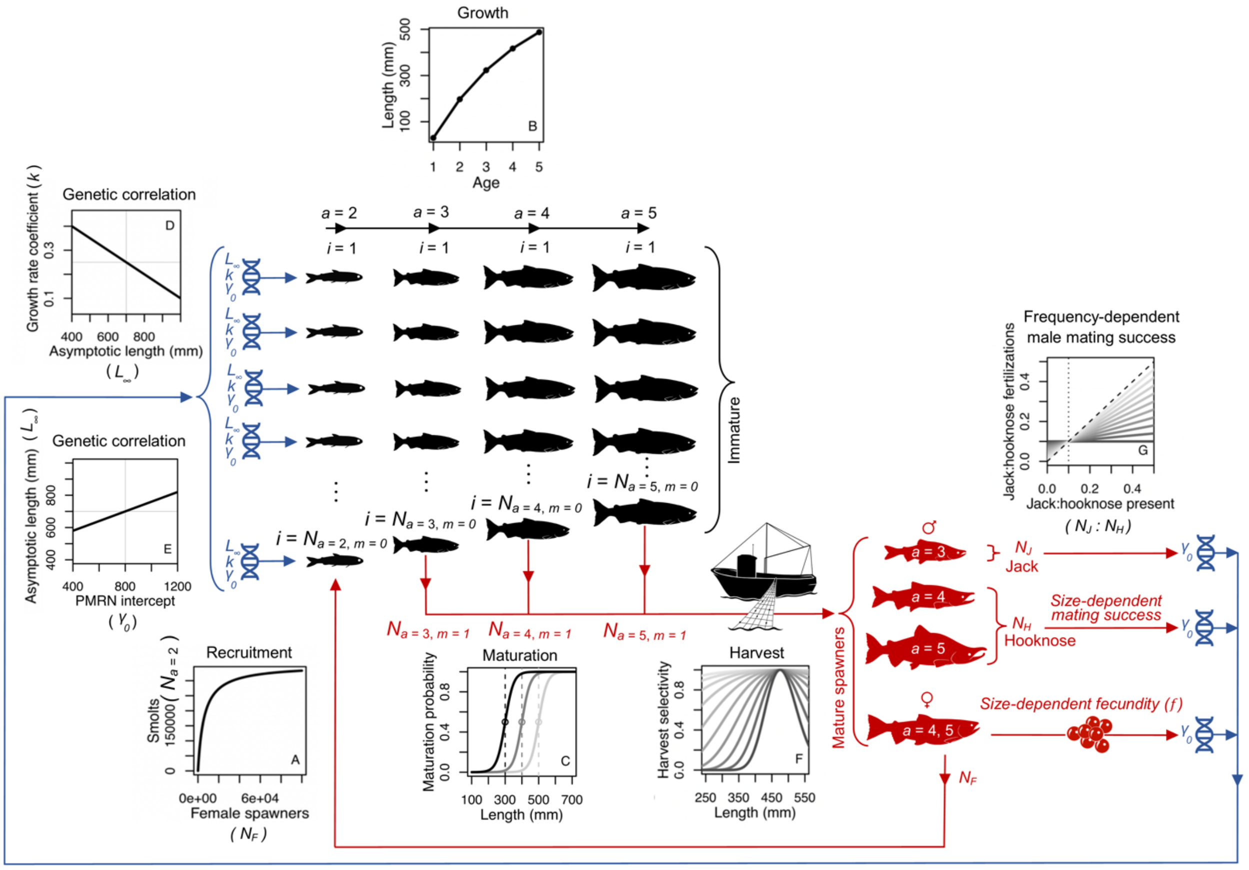

Figure 3.1. Simulation model functions and dynamics. In the flow chart, immature fish are shown in black, mature fish are shown in red, and genetic processes and traits are shown in blue. Individuals (i) are added to the population as age-2 ($a = 2$) sexually immature ($m = 0$) smolts. The number of smolts produced each year ($N_{a=2,m=0}$) is determined by a Beverton-Holt function of female spawner abundance two years prior (N_F). The deterministic portion of the spawner-recruit relationship is shown in panel A. Each year, individuals transition into the next age class and grow according to a von Bertalanffy curve (panel B) as determined by their values for growth rate (k) and asymptotic size (L_∞), which are genetically determined. Each year a portion of immature individuals die due to natural mortality according to age-specific survival probabilities (s_a) and mature ($m = 1$), with a probability determined by their length, age, and probabilistic

maturation reaction norm (PMRN) intercept (γ_0). Panel C shows the maturation probability as a function of length for age-3 (light grey), age-4 (medium grey), and age-5 individuals (black) where the dashed line and open circles represent the length at which the maturation probability is 50% for each age class under reference value for γ_0. The intercept of the PMRN (γ_0) is inherited from an individual's same sex parent, and L_∞ is determined through an assumed genetic correlation with γ_0 (panel E). Similarly, k is determined through an assumed correlation with L_∞ (panel D). Individuals reaching maturity in a given year are exposed to harvest with a range of fishery selectivity curves from strongly size-selective (dark gray) to size-unselective (lighter gray) (G). Mature individuals that survive the fishery form the spawning escapement. The number of females in the escapement determines the number of offspring produced (in addition to stochastic variation, not shown here), and the number of offspring produced by each individual female is determined by her relative body size. Of the males in the escapement, the relative reproductive success of jacks ($a = 3$) versus hooknose males ($a = 4, 5$) is determined by a linear negatively frequency-dependent mating function. This function is shown in panel F, where the x axis shows the ratio of jacks to hooknoses present in the spawning population and the y axis depicts the ratio of eggs fertilized by each. The dashed line represents the 1:1 line at which the reproductive success of each tactic would be directly proportional to its frequency in the population, and the dotted line shows the equilibrium ratio at which this is occurs for the functions shown ($\mu = 0.1$). The solid lines show varying slopes of the frequency-dependent function ranging from low values ($\theta_{FDS} = 0$), which represent strong negative frequency-dependent mating (black) to high values ($\theta_{FDS} = 0.9$) representing weaker frequency-dependence (light grey). While frequency dependence determines the total reproductive success of hooknose males versus jacks, among hooknose males, an individual's reproductive success is also proportional to its body size relative to that of other hooknose males. Mature individuals that successfully reproduce pass their genetic trait values for γ_0 (plus mutation-segregation error) onto their offspring, allowing the population to evolve over time.

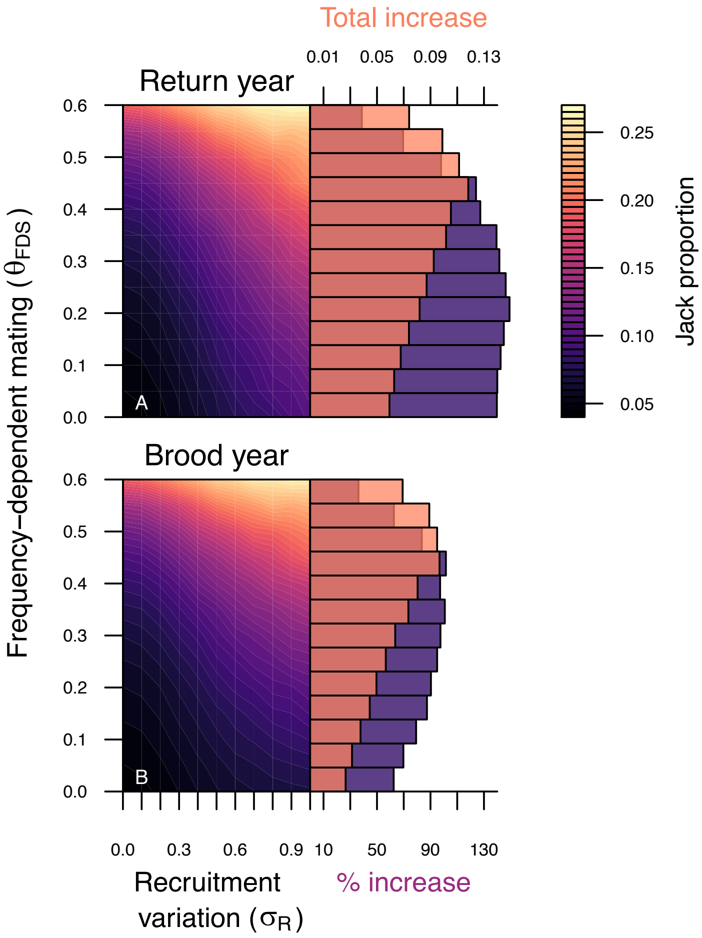

Figure 3.2. Contours of average jack prevalence across levels of recruitment variation and frequency-dependent mating. Panels shows jack prevalence by return year (Panel A), and by brood

year (Panel B) year in the final 200 years of the simulation across levels of recruitment variation (σ_R= 0.0-1.0), and values of negatively frequency-dependent reproductive success (θ_{FDS}). The range of values for frequency-dependence considered here was truncated to include only values that did not result in the majority of males becoming jacks ($\theta_{FDS} \leq 0.6$). Results shown here are for intermediate values of growth variation (σ_G= 0.2) and equilibrium mating frequencies ($\mu = 0.01$). Adjoining histograms show the relative (transparent purple) and absolute (transparent orange) increase in jack prevalence from equilibrium conditions ($\sigma_R = 0$) to the highest level of recruitment variation considered ($\sigma_R = 1$) for a given level of frequency-dependence.

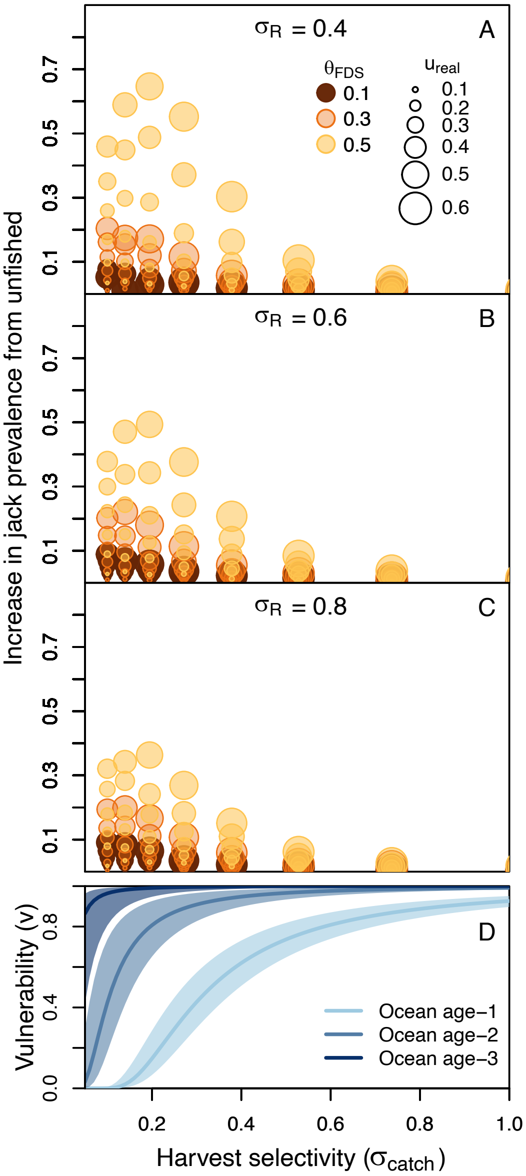

Figure 3.3. Effects of harvest on the prevalence of jacks. Panels A-C show the absolute increase in jack prevalence associated with different levels of fishing mortality and size-selectivity (x axis) relative to an unfished state in the same biological parameter space. The size of the dots represents the median across simulations of the average realized exploitation rate (u_{real}) at a given levels of harvest selectivity (σ_{catch}) re-calculated from specified target exploitation rates

from 0.1 to 0.6. Because the realized harvest rates changed over time as the age-composition shifted, these exploitation rates are calculated during the first ten years of harvest, prior to any significant shifts. The color of the dots represents the different levels of frequency-dependent mating that were considered (θ_{FDS}), with the yellow dots showing modest levels of frequency dependence ($\theta_{FDS} = 0.5$), the orange dots showing scenarios of $\theta_{FDS} = 0.3$, and the brown dots showing the strongest levels of frequency-dependence considered ($\theta_{FDS} = 0.1$). Panel A shows the results for low levels of recruitment variation ($\sigma_R = 0.4$), panel B shows results for intermediate levels of recruitment variation ($\sigma_R = 0.6$) and panel C shows results for high recruitment variation ($\sigma_R = 0.8$). Panel D shows the expected vulnerability of each ocean age class at a given level of harvest selectivity (σ_{catch}) according to the projected size-at-age of the von-Bertalanffy growth function with the reference values $L_{\infty}^{ref} = 700$ and $k^{ref} = 0.25$. Solid lines show the projected vulnerability to harvest for the deterministic sizes of ocean age-1 (light blue), ocean age-2 (medium blue), and ocean age-3 (dark blue) fish. Transparent boundaries show the 25th and 75th quantiles of the size distribution of each age class according to the level of growth variation assumed in these simulations ($\sigma_G = 0.2$).

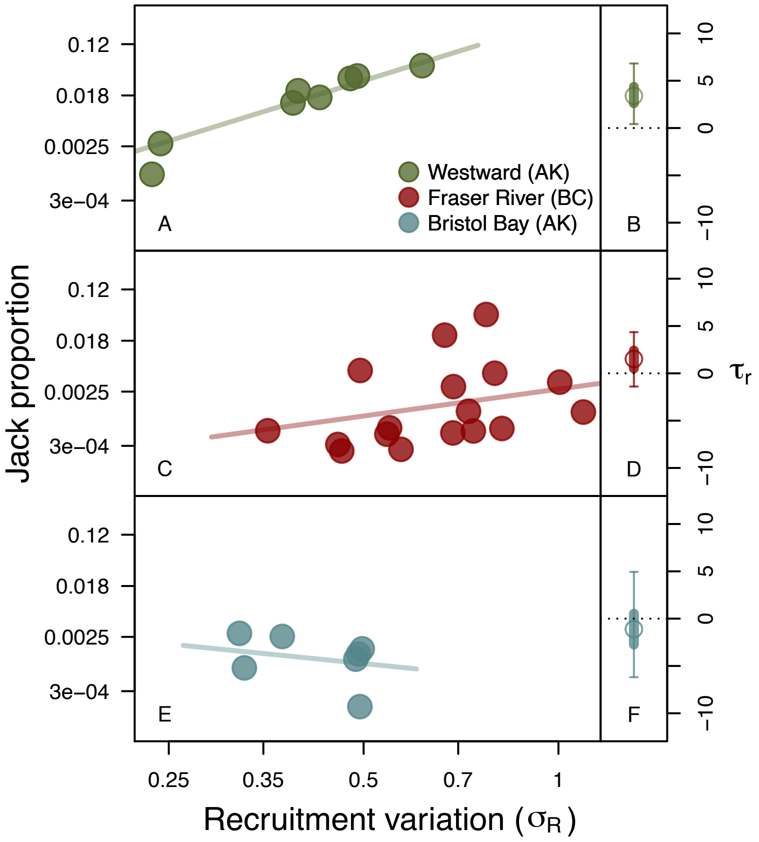

Figure 3.4. Estimated relationships between population recruitment variability (σ_R) and jack prevalence by region. Panels A-C show the relationships between recruitment variation and a population's estimated average jack prevalence (dots) and the solid line shows the predicted relationship for a given region. Panels D-F show the estimated posterior distribution of the coefficient relating recruitment variation and jack prevalence (τ_r) where the thin lines show the 95% credible intervals, the thick lines are the 50% credible intervals, and the circle shows the median.

SYNTHESIS

In this dissertation, I have examined how discrete life history variation is maintained within populations and explored implications for fisheries management. I have evaluated data from natural populations within the context of evolutionary theory and find both support for, and incongruencies with, existing frameworks. I have found evidence consistent with expectations that precocious jacks in sockeye salmon populations should be more common in populations where the survival advantage of a curtailed marine residency and smaller body size are greater, and where habitat conditions are more suitable for sneak spawning (Gross 1991). These findings support the role of adaptive evolution and frequency-dependent selection in shaping the frequencies of alternative life histories within a population. However, in Chapters Two and Three, my results challenge the expectation that frequencies of alternative male phenotypes in a population are purely a reflection of their underlying fitness functions. Instead, I find compelling evidence to suggest that population dynamics are a salient factor in shaping the frequencies of alternative life histories in salmon, and perhaps in age-structured populations more generally.

Because of the differences in age-at-maturity between male phenotypes, interannual variation in cohort strength necessarily induces variation in the ratio of jacks to hooknose males on the spawning grounds. Such ‘cohort mismatches’ decouple an individual’s realized fitness payoffs from its maturation genotype and should prevent the population from reaching an evolutionarily stable state (Koseki and Fleming 2006; 2007). Such disruption acts to even out the distribution of life histories in the population, which, because jacks are the rarer tactic, has the effect of increasing their prevalence (Chapter Three). This mechanism, in conjunction with size-selective harvest, appears responsible for an increase in the prevalence of jacks in Frazer Lake sockeye salmon (Chapter 2). My simulation results from chapter three indicate that both evolutionary (frequency-dependent mating), and population dynamic (recruitment variation) factors are important to shaping a population's realized jack prevalence. Similarly, the data examined in Chapter Three indicate a relationship between a population's recruitment variation and its jack prevalence in some, but not all regions, providing further evidence that both evolutionary and population dynamic factors are likely important. Collectively, these results demonstrate that population dynamics and sexual selection can interact to produce emergent dynamics that could not be predicted from purely evolutionary models.

From a fisheries standpoint, large increases in the prevalence of jacks can be problematic, as jacks presently have little commercial or recreational value. My results suggest that size-selective harvest can lead to increases in the prevalence of jacks (chapter 2, 3). However, simulation results from chapter three show that frequency-dependent mating filters how populations respond to fisheries-induced selection. This finding potentially explains why large increases in jack prevalence in exploited salmon populations are rare despite extensive long-term monitoring data and extensive histories of size-selective exploitation on many salmon populations. Furthermore, it suggests that empirical estimates of the strength of frequency-dependent mating (e.g. Berejikian et al. 2010) is critical in determining how populations are likely to respond to size-selective exploitation. More generally, this result emphasizes the importance of considering multiple patterns of selection in studies of fisheries-induced evolution.

Collectively, the results of this dissertation are informative to our understanding of salmon life histories and fisheries management, and provide lessons that are applicable to evolutionary biology and natural resource science more broadly. There are several characteristics of sockeye salmon biology that seem to contribute to the 'cohort mismatch' phenomenon, including semelparity, age structure, heritability of mating/maturation phenotypes, and somewhat limited age diversity within jack (ocean age-1), and hooknose male (ocean age-2,3) life history categories. While there is freshwater age diversity, most populations typically have a single dominant freshwater age, which increases the probability that year-to-year variation in recruitment strength will cause a cohort mismatch. Importantly, while this dissertation was focused on the effects of recruitment variation on shaping alternative life histories subject to frequency-dependent selection, the findings may be more generally applicable. In any age-structured population, substantial interannual variation in recruitment strength will affect the standing age distribution of the breeding population. As such, to the extent that age-at-maturity is heritable, recruitment variation may act to even out the distribution of maturation genotypes in the population, and serve to maintain diverse life history portfolios. I strongly recommend that future studies explore this interesting and potentially far-reaching hypothesis.

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APPENDIX A: CHAPTER 1

Table A1. Rank order of median posterior estimates of jack prevalence among stream populations from model 5 fitted to age composition data by return versus brood year. Some populations lacked sufficient data to reconstruct brood year age composition at all (indicated by N/A).

Population Name	Rank Order by Return Year	Rank Order By Brood Year
Nerka Teal Creek	1	2
Aleknagik Eagle Creek	2	3
Aleknagik Big Whitefish Creek	3	1
Aleknagik Hansen Creek	4	4
Aleknagik Mission Creek	5	6
Nerka Pike Creek	6	11
Aleknagik Yako Creek	7	7
Nerka Sam Creek	8	9
Nerka Berm Creek	9	5
Nerka Hidden Lake Creek	10	8
Nerka Lynx Creek	11	13
Nerka Allah Creek	12	N/A
Beverley Moose Creek	13	16
Little Togiak C Creek	14	N/A
Nerka Joe Creek	15	10
Nerka Stovall Creek	16	14
Aleknagik Happy Creek	17	17
Little Togiak A Creek	18	N/A
Nerka Fenno Creek	19	15
Aleknagik Bear Creek	20	12
Nerka Kema Creek	21	18
Aleknagik Ice Creek	22	20
Nerka Pick Creek	23	19
Beverley Uno Creek	24	N/A

Table A2. Rearing lake, spawning habitat type, and data availability associated with each population. The ‘Otolith’ column indicates the availability of age composition estimates based on otoliths extracted during carcass surveys, the ‘Live Count’ column indicates estimates of jack prevalence based on live censuses, the ‘SNPs’ column indicates the availability of neutral genetic data, the ‘Length-at-age’ column indicates length-at-age data, and the ‘Behavior’ column indicates whether behavioral observations were performed. ‘Y’ indicates that a data type is available for that population, while ‘N’ indicates that it is not available.

Population	Rearing Lake Basin	Spawning Ecotype	Otolith	Live Count	SNPs	Length-at-Age	Behavior
Teal Creek	Nerka	Stream	Y	Y	Y	Y	N
Eagle Creek	Aleknagik	Stream	Y	Y	Y	Y	N
Big Whitefish Creek	Aleknagik	Stream	Y	Y	Y	Y	N
Hansen Creek	Aleknagik	Stream	Y	N	Y	Y	N
Mission Creek	Nerka	Stream	Y	Y	N	Y	N
Pike Creek	Nerka	Stream	Y	Y	N	Y	N
Yako Creek	Aleknagik	Stream	Y	Y	N	Y	N
Sam Creek	Nerka	Stream	Y	Y	N	N	N
Berm Creek	Nerka	Stream	Y	Y	N	N	N
Hidden Lake Creek	Nerka	Stream	Y	Y	N	Y	Y
Lynx Creek	Nerka	Stream	Y	Y	Y	Y	Y
Allah Creek	Nerka	Stream	Y	Y	N	N	N
Moose Creek	Beverley	Stream	Y	Y	Y	N	N
C Creek	Little Togiak	Stream	Y	N	N	Y	N
Joe Creek	Nerka	Stream	Y	Y	Y	N	N
Stovall Creek	Nerka	Stream	Y	Y	Y	Y	N
Happy Creek	Aleknagik	Stream	Y	Y	Y	Y	N
A Creek	Little Togiak	Stream	Y	N	N	Y	N
Fenno Creek	Nerka	Stream	Y	Y	N	Y	Y
Bear Creek	Aleknagik	Stream	Y	Y	Y	Y	N
Kema Creek	Nerka	Stream	Y	Y	Y	Y	N
Ice Creek	Aleknagik	Stream	Y	Y	N	Y	N
Pick Creek	Nerka	Stream	Y	Y	Y	Y	N
Uno Creek	Berverley	Stream	Y	N	Y	N	N
Hardluck Bay Beach	Beverley	Lake Beach	Y	N	N	Y	N
Silver Horn Beach	Beverley	Lake Beach	Y	N	N	N	N
B9-B12 Beach	Beverley	Lake Beach	Y	N	N	N	N
Kulik Beaches	Kulik	Lake Beach	Y	N	N	N	N
N4-N6 Beaches	Nerka	Lake Beach	Y	N	N	N	N
Little Togiak Beaches	Little Togiak	Lake Beach	Y	N	N	N	N
Anvil Bay Beach	Nerka	Lake Beach	Y	N	N	N	N
Wood River	Aleknagik	River	Y	N	N	Y	N
Grant River	Kulik	River	Y	N	N	N	N
Little Togiak River	Nerka	River	Y	N	N	N	N
Agulukpak River	Nerka	River	Y	N	N	N	N
Agulowak River	Aleknagik	River	Y	N	N	Y	N

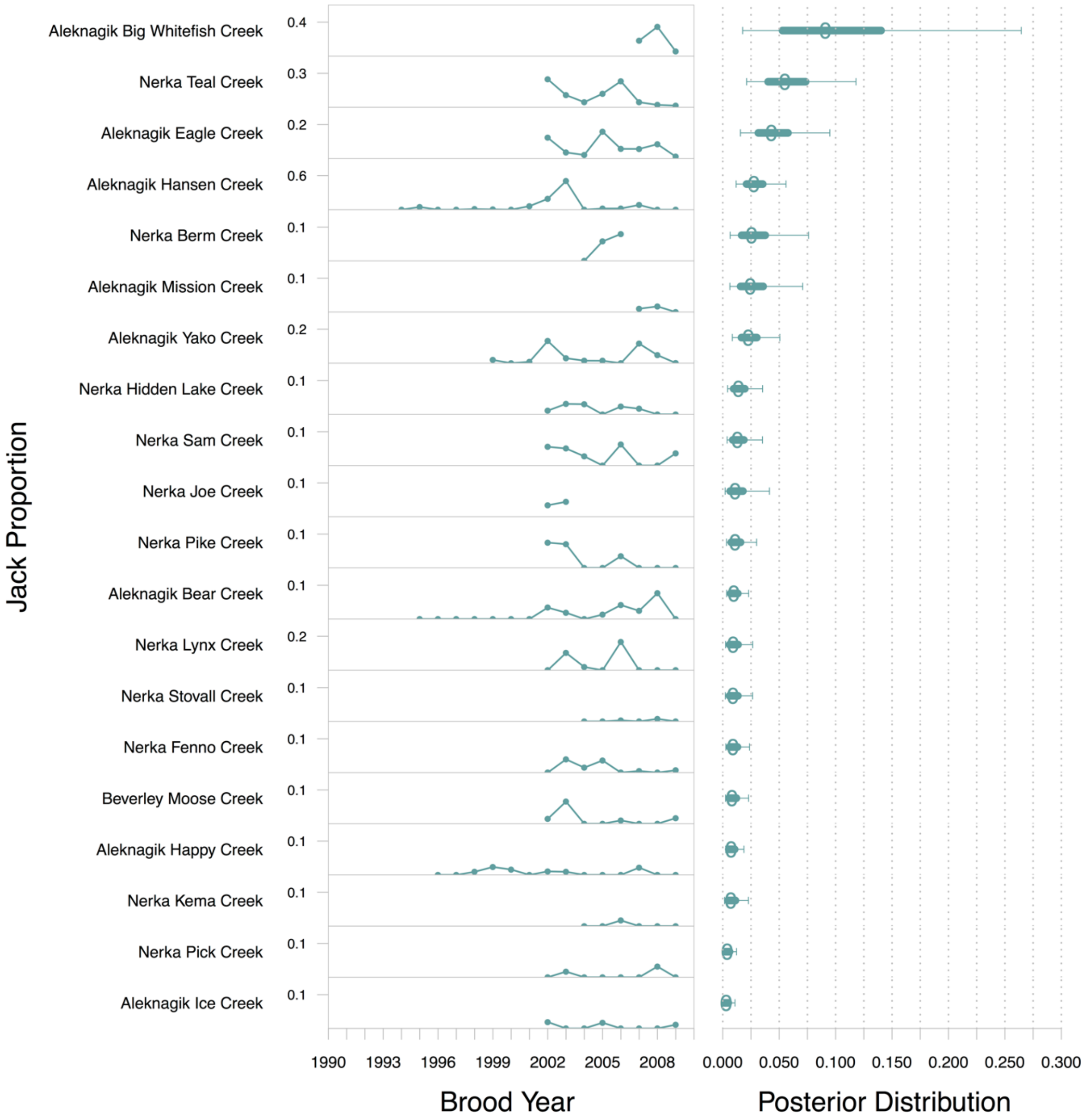


Figure A1. Patterns of jack prevalence by brood year across stream populations. Sparklines depict the temporal patterns of jack proportions for each population. To fully reconstruct the male age composition of a given brood year, several years of uninterrupted, sex-specific age composition and abundance data by return year are needed. Due to variability in the consistency of surveys, sufficient data for complete brood reconstructions was limited.

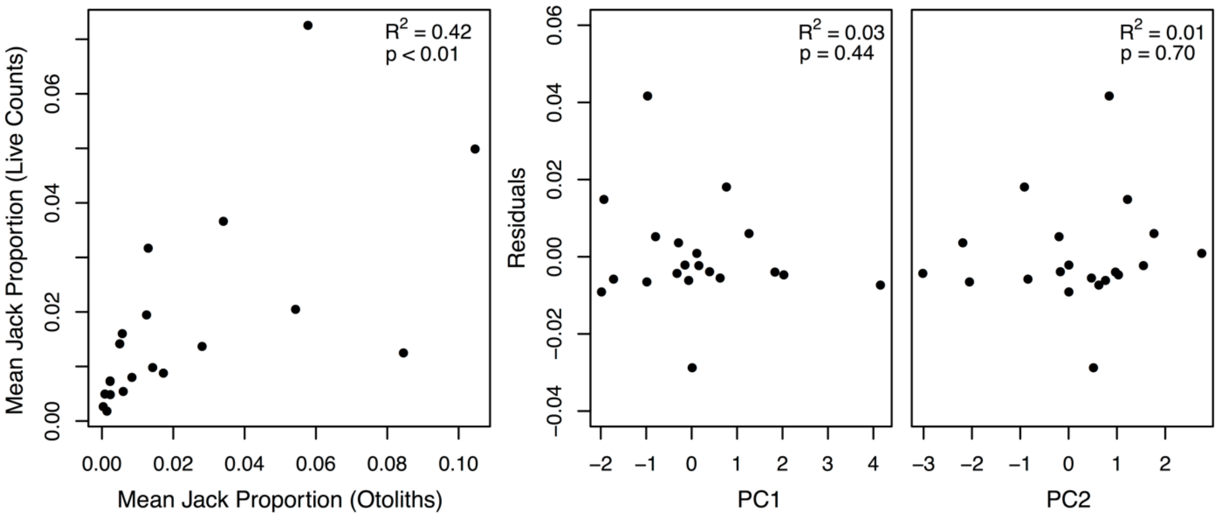


Figure A2. Evaluating a potential geomorphic basis for carcass sampling bias. Panel 1 depicts the relationship between average jack prevalence among populations based on otoliths collected during carcass surveys versus those identified visually during counts of live individuals. Panels 1 and 2 show the relationship between the residuals of this regression and principal components 1 (PC1) and 2 (PC2) respectively.

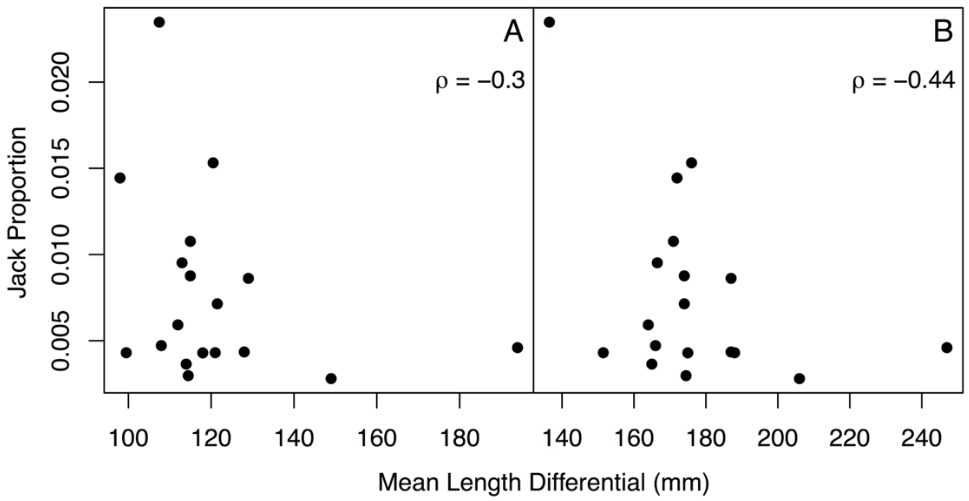


Figure A3. Relationship between median posterior estimates of jack prevalence and the mean length differential between jacks and ocean age two (A) and ocean age three (B) fish.

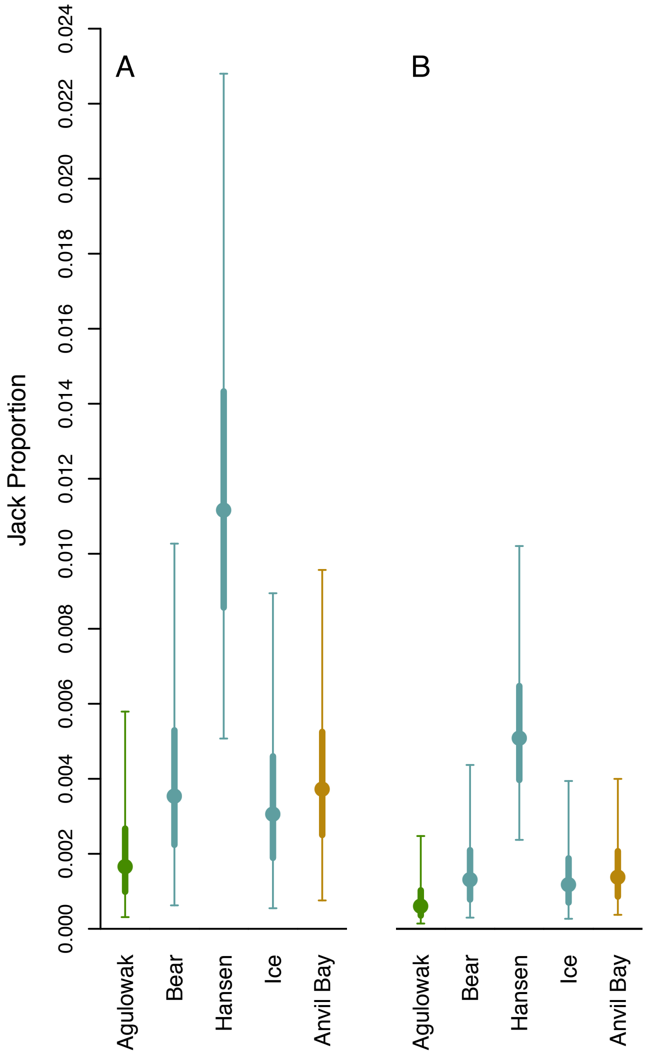


Figure A4. Comparison of posterior distributions for population jack proportions without adjusting for fishery exploitation (A) and after adjusting for population specific exploitations rates (B), assuming jacks comprise a negligible portion of the catch. Posterior distributions are based off of a version of model 3 fitted only to these five populations for which exploitation rates were calculated previously by Kendall and Quinn 2009. Stream populations are pictured in blue, rivers in green, and beaches in brown.

APPENDIX B: CHAPTER 2

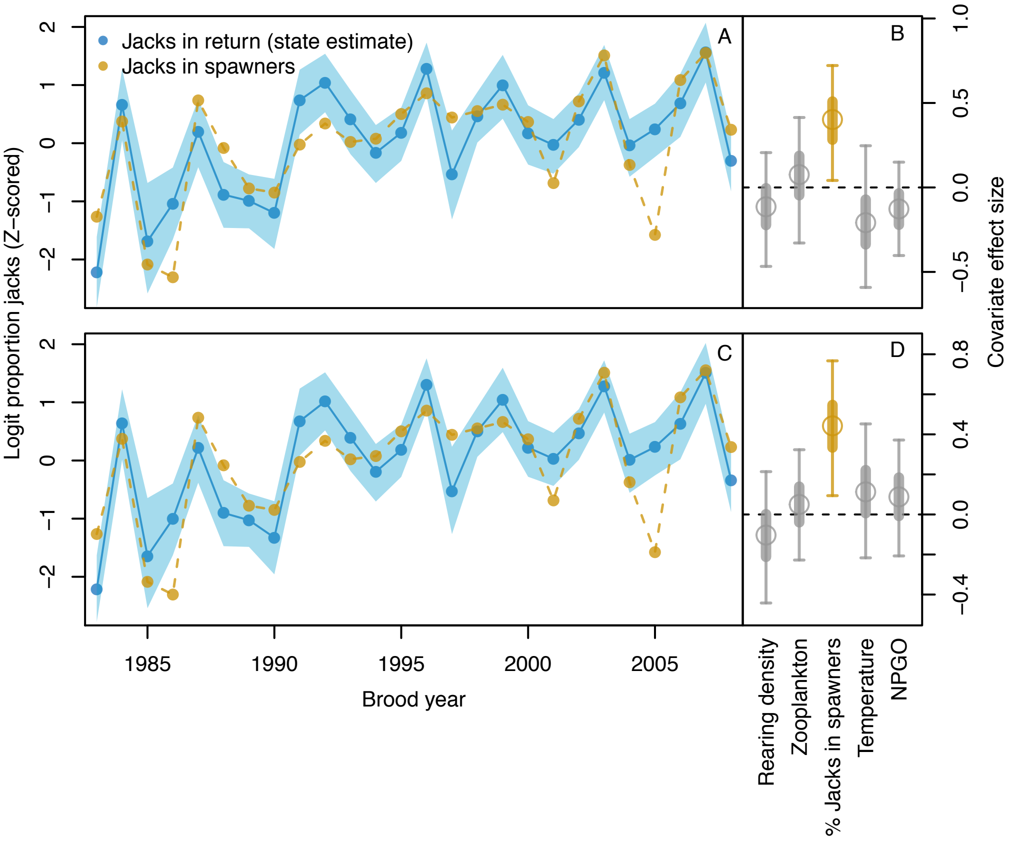


Figure B1. Sensitivity of state estimates and covariate effect sizes to alternative lags and moving average windows. In panels A-B, temperature is specified as a moving average of the current year and the next year to capture potential effects of temperature on developing eggs and fry, NPGO is shifted forwards by two years, and zooplankton biomass is set as a 2-year moving average, shifted forwards by 1 and 2 years (as in the main figure). In panels C-D, temperature and zooplankton biomass are both shifted forwards by 2 years to capture their effects towards the end of freshwater residency, and NPGO is shifted forward by 3 years.

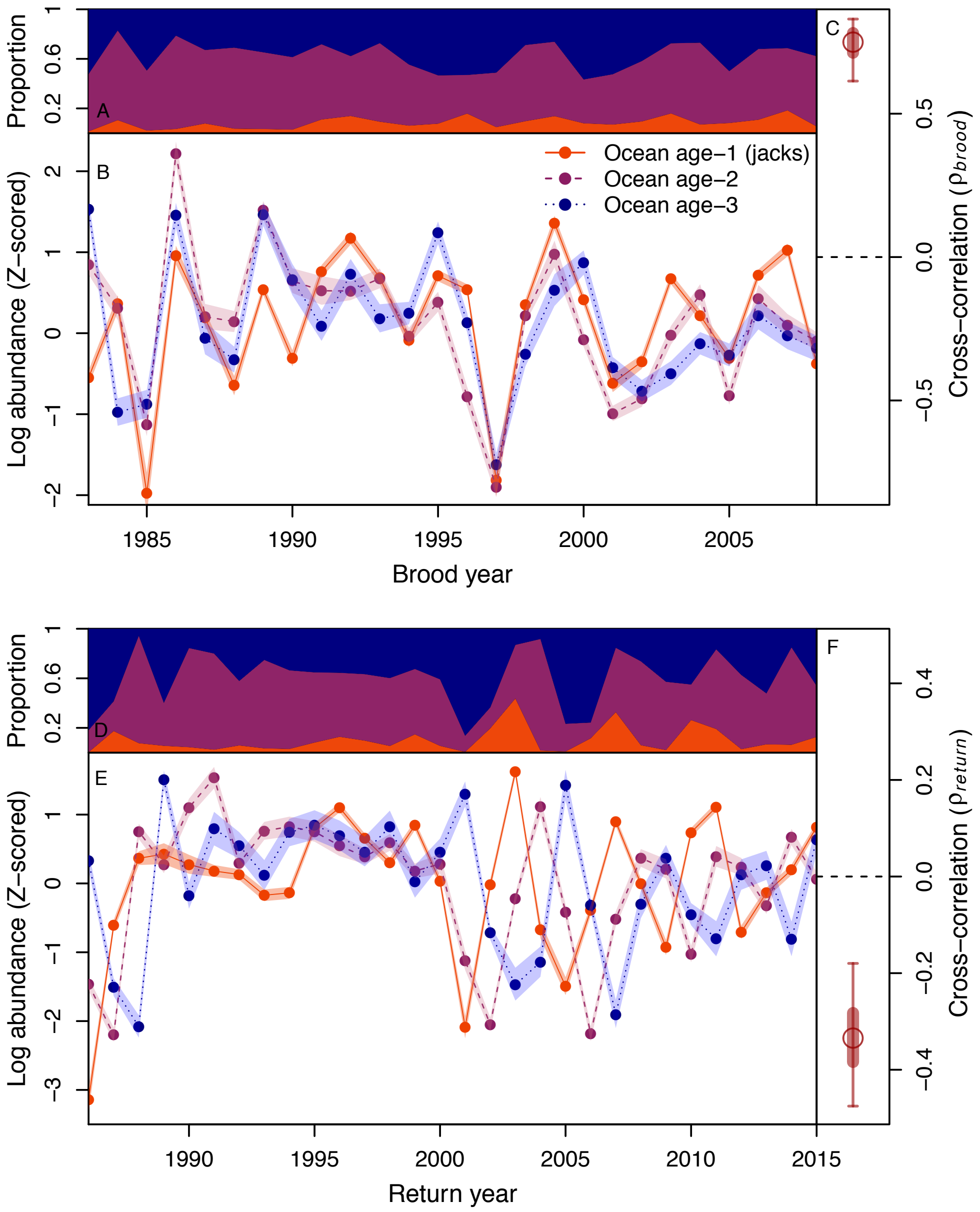


Fig B2. Results of figure 2.5 based on output generated solely from the model represented by eq. 2. (goal 1) As in figure 2.5 in the main text, panels A and D show the posterior median estimates of the proportions of ocean age-1, 2, and 3 fish by brood year (A) and return year (D). Panels B and E depict Z-scored state estimates of the log abundance of ocean age-1, 2, and 3 fish by brood year (B) versus return year (E). Posterior medians are indicated by solid dots, while the 50% credible intervals are indicated as transparent boundaries. Panels C and F depict the posterior distribution of the cross-correlation coefficient between jacks (ocean age-1), and the hooknose age classes (ocean age-2 plus ocean age-3) by brood year (ρ_{brood}) and return year (ρ_{return}). The posterior median is indicated by a circle, while the 50% and 95% credible intervals are represented by thick and thin lines respectively.

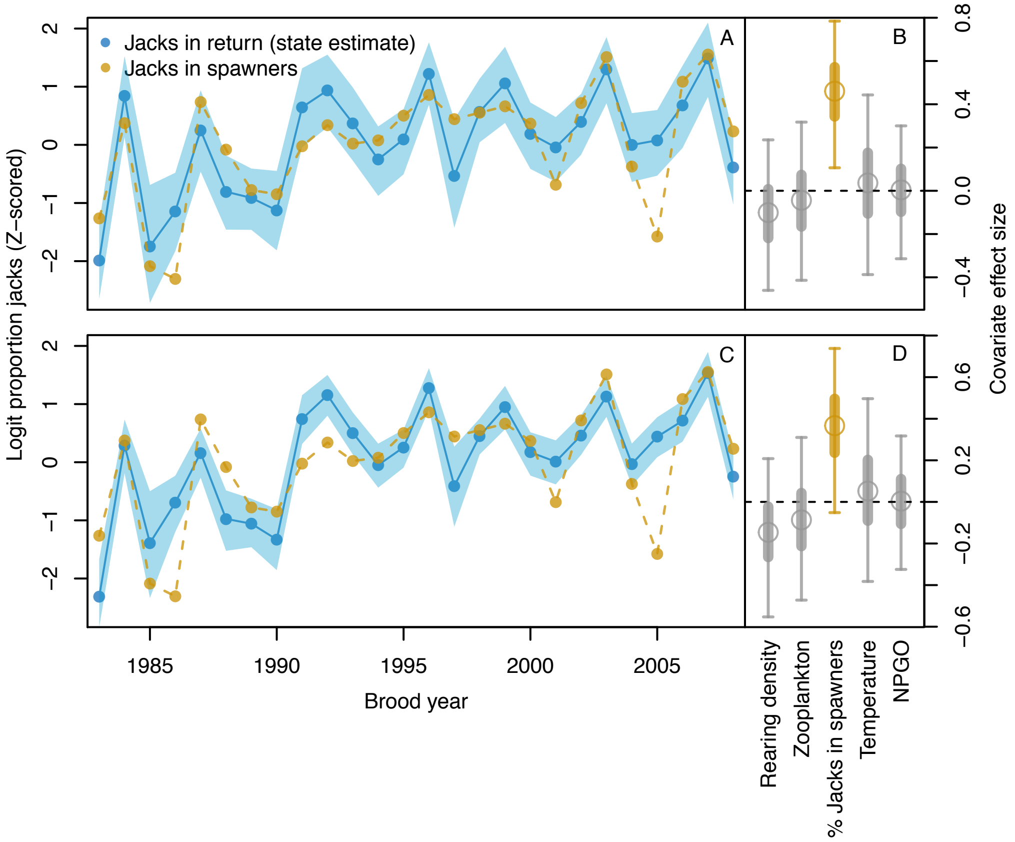


Figure B3. Sensitivity of state estimates and covariate effect sizes to alternative values of observation error variance for the harvest and escapement counts. Panels A and B represent the results of Figure 3 with higher observation error (σ_C = 0.75, σ_E = 0.15), while panels C and D represent the results under a lower observation error scenario (σ_C = 0.25, σ_E = 0.05).

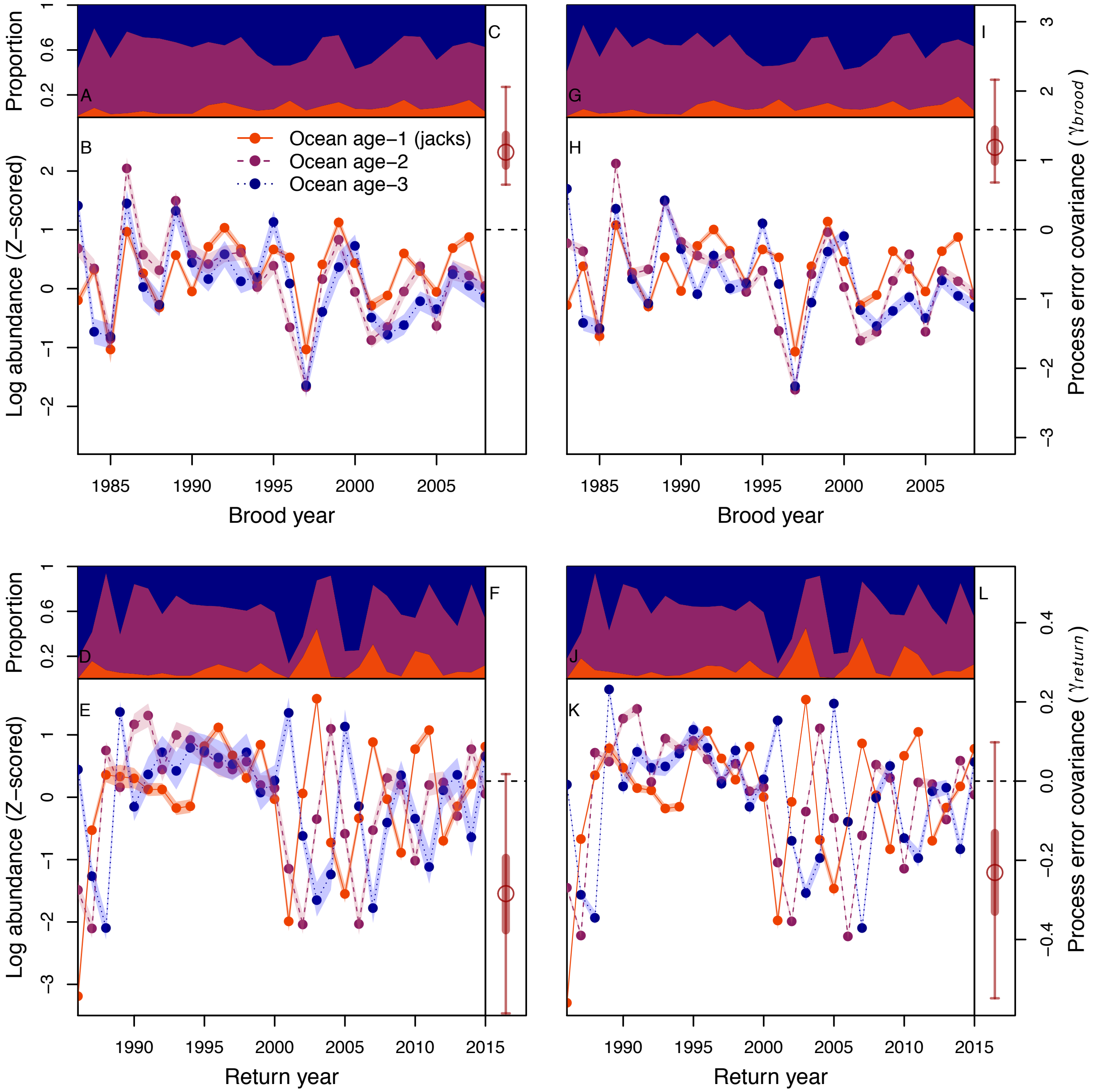


Figure B4. Sensitivity of state and covariance estimates to alternative values of observation error variance for the harvest and escapement counts. Panels A through F represent the results of figure 5 with higher observation error ($\sigma_C = 0.75$, $\sigma_E = 0.15$), while panels G through L represent the results under a lower observation error scenario ($\sigma_C = 0.25$, $\sigma_E = 0.05$).

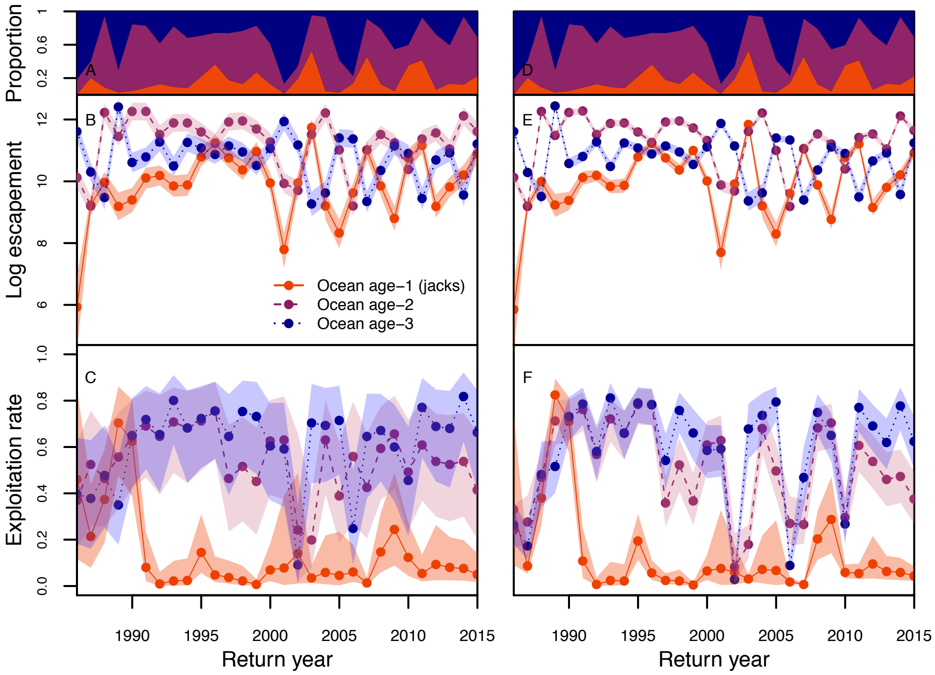


Figure B5. Sensitivity of harvest and escapement estimates to alternative values of observation error variance for harvest and escapement counts. Panels A through C represent the results of Figure 6 with higher observation error ($\sigma_C = 0.75$, $\sigma_E = 0.15$), while panels D through F represent the results under a lower observation error scenario ($\sigma_C = 0.25$, $\sigma_E = 0.05$).

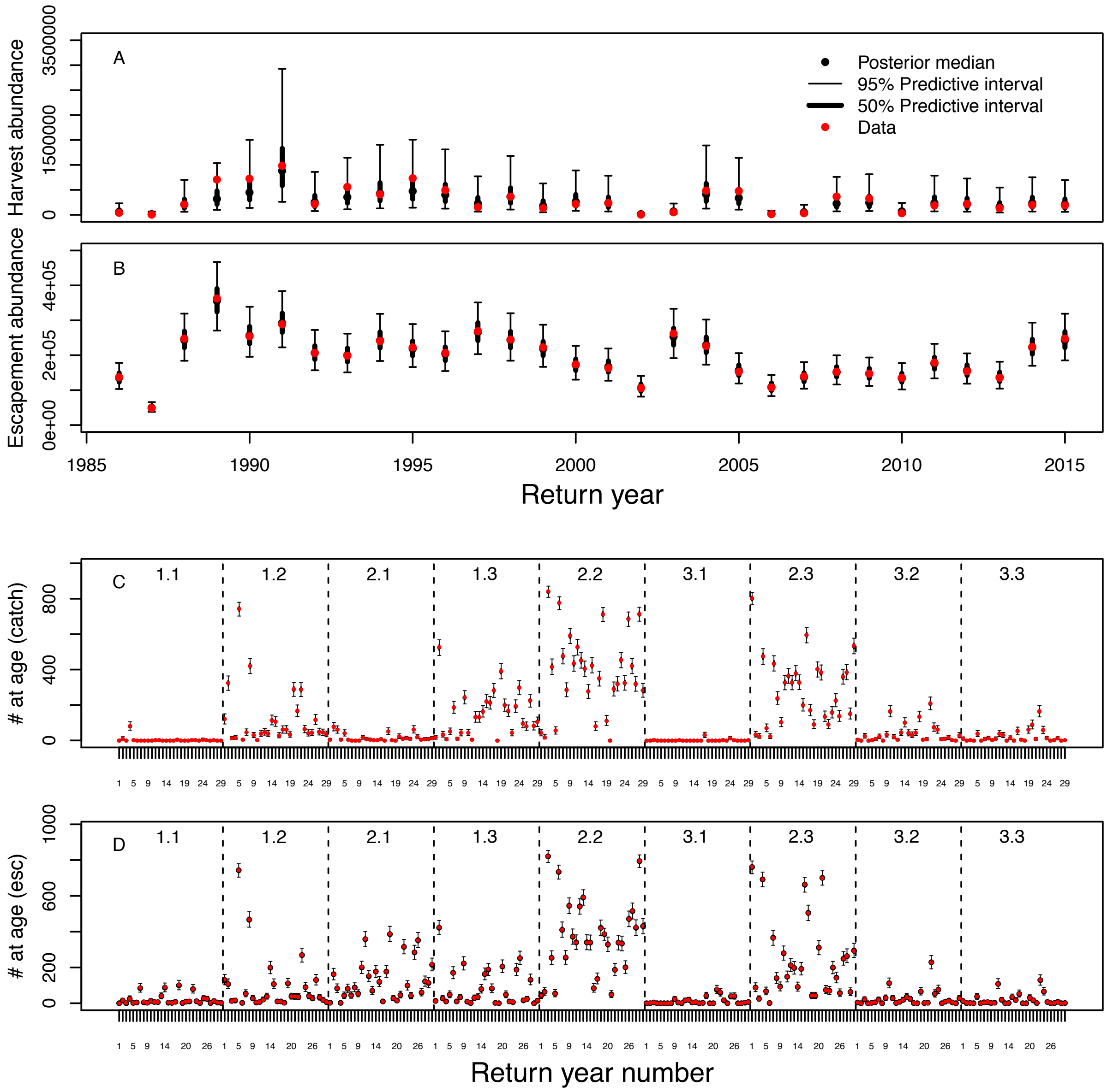


Figure B6. Posterior predictive check for the univariate model of brood year jack proportions (eq. 2.2). Panels A and B depict the predictive distributions relative to the observed data for the harvest and escapement abundance respectively. Panels C and D depict the predictive distributions relative to the observed data for the age composition of the harvest and escapement respectively. The predictive distributions for each age group across all years are separated by dotted lines. The labels represent freshwater and marine age separated by a decimal.

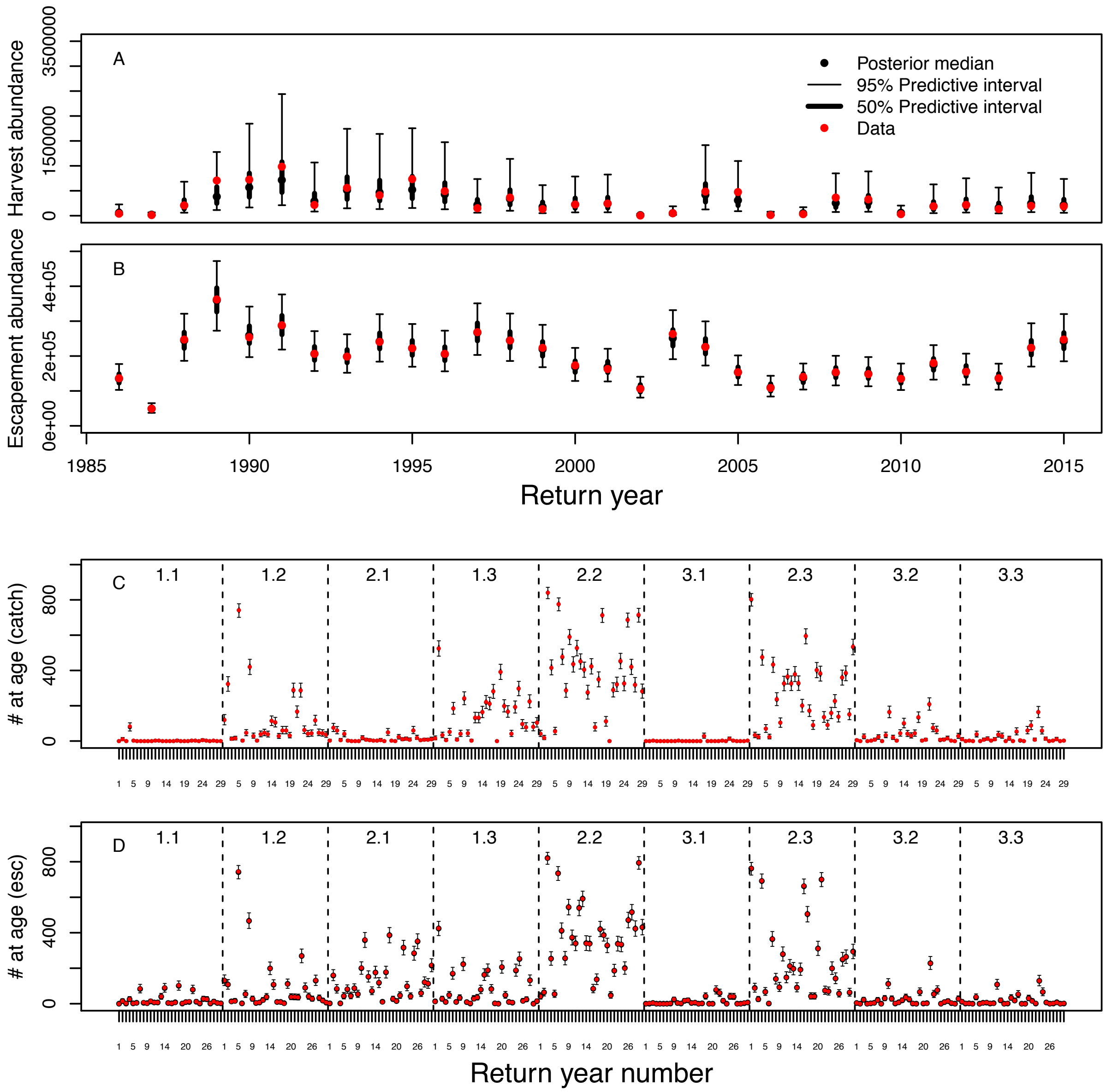


Figure B7. Posterior predictive check for the multivariate model of return year abundance of ocean age classes (eq. 2.11). Panels A and B depict the predictive distributions relative to the observed data for the harvest and escapement abundance respectively. Panels C and D depict the predictive distributions relative to the observed data for the age composition of the harvest and escapement respectively. The predictive distributions for each age group across all years are separated by dotted lines. Labels represent freshwater and marine age separated by a decimal.

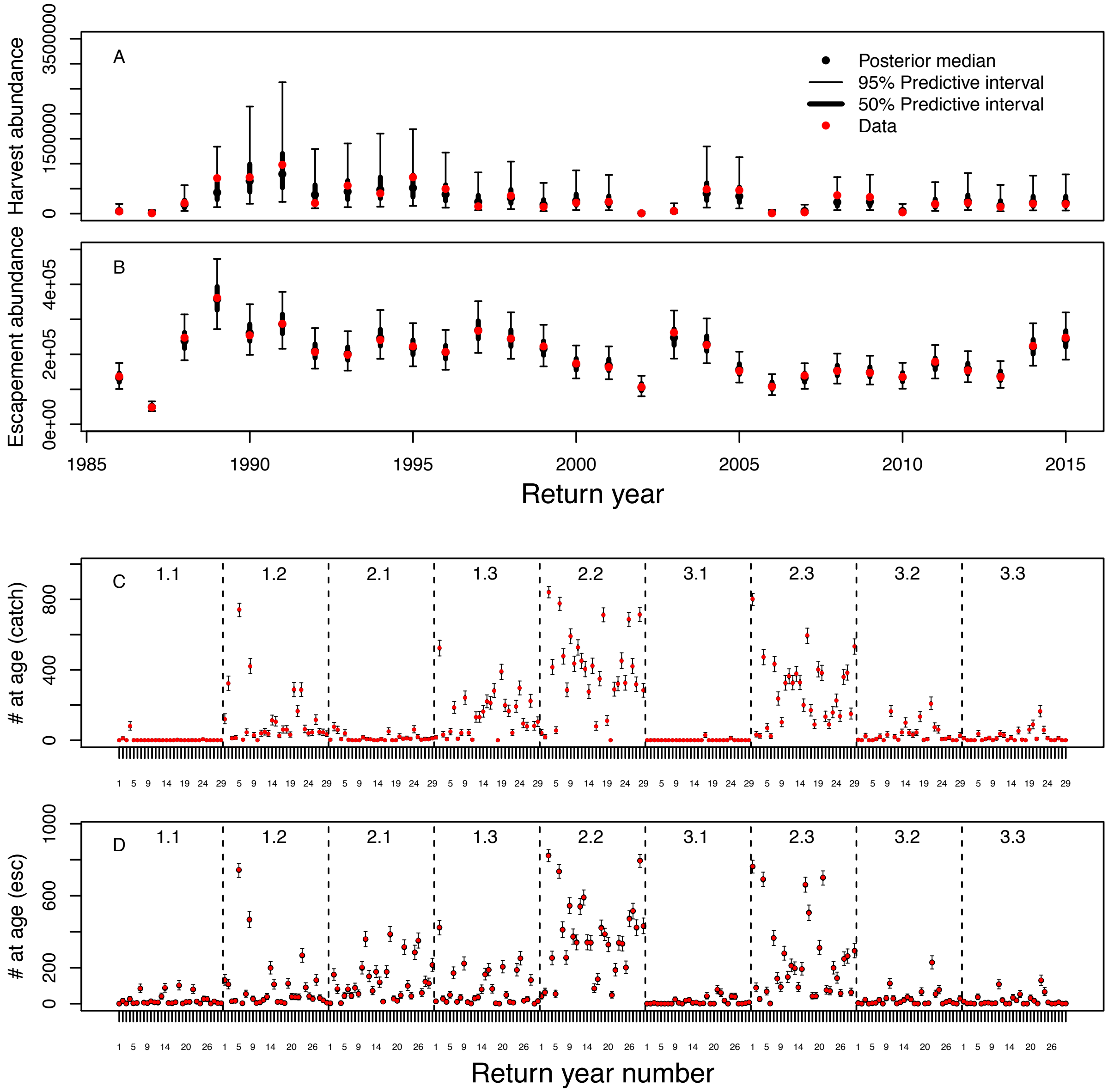
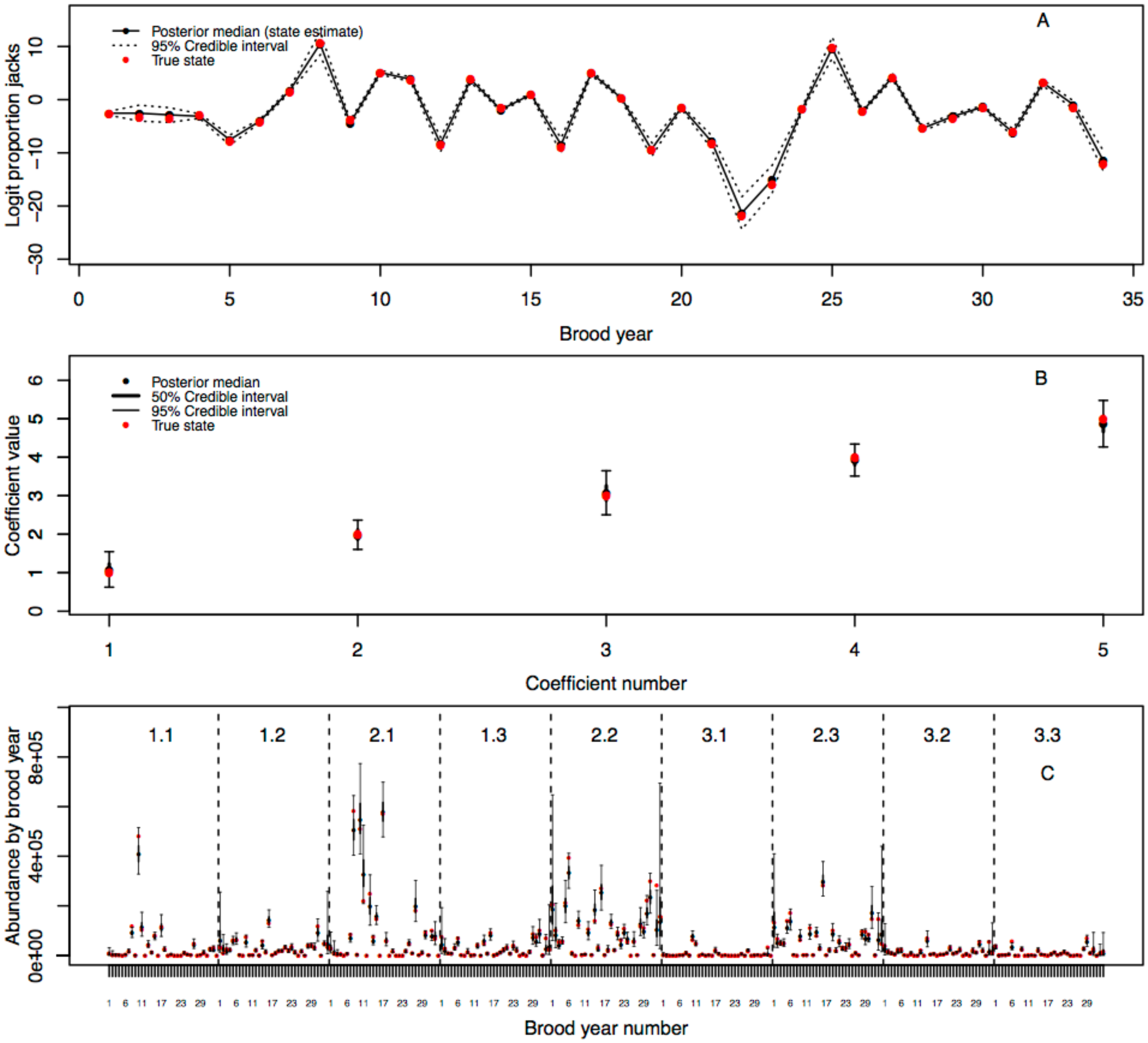


Figure B8. Posterior predictive check for the multivariate model of brood year abundance of ocean age classes (eq. 2.10). Panels A and B depict the predictive distributions relative to the observed data for the harvest and escapement abundance respectively. Panels C and D depict the predictive distributions relative to the observed data for the age composition of the harvest and escapement respectively. The predictive distributions for each age group across all years are separated by dotted lines. Labels represent freshwater and marine age separated by a decimal.



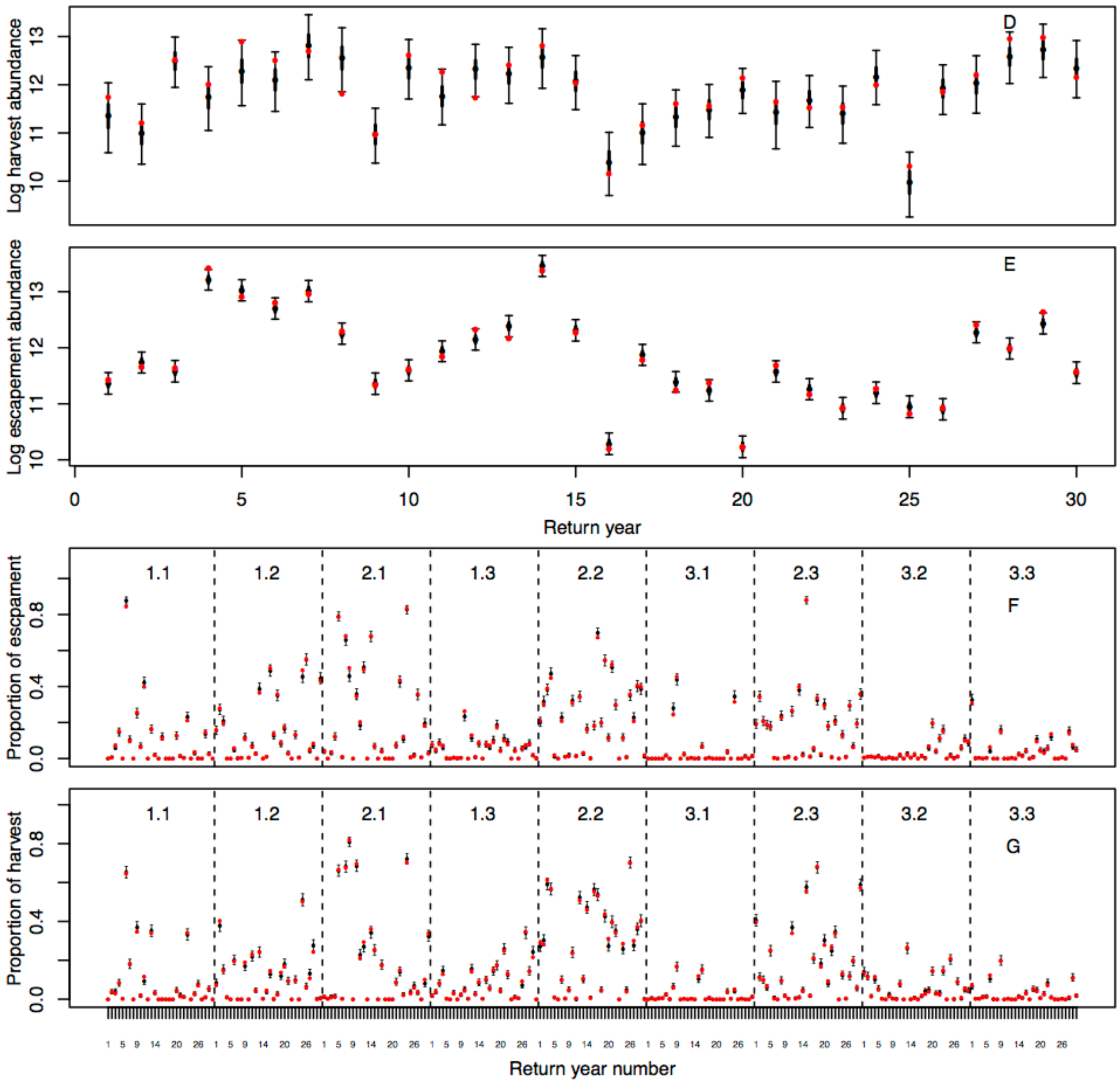
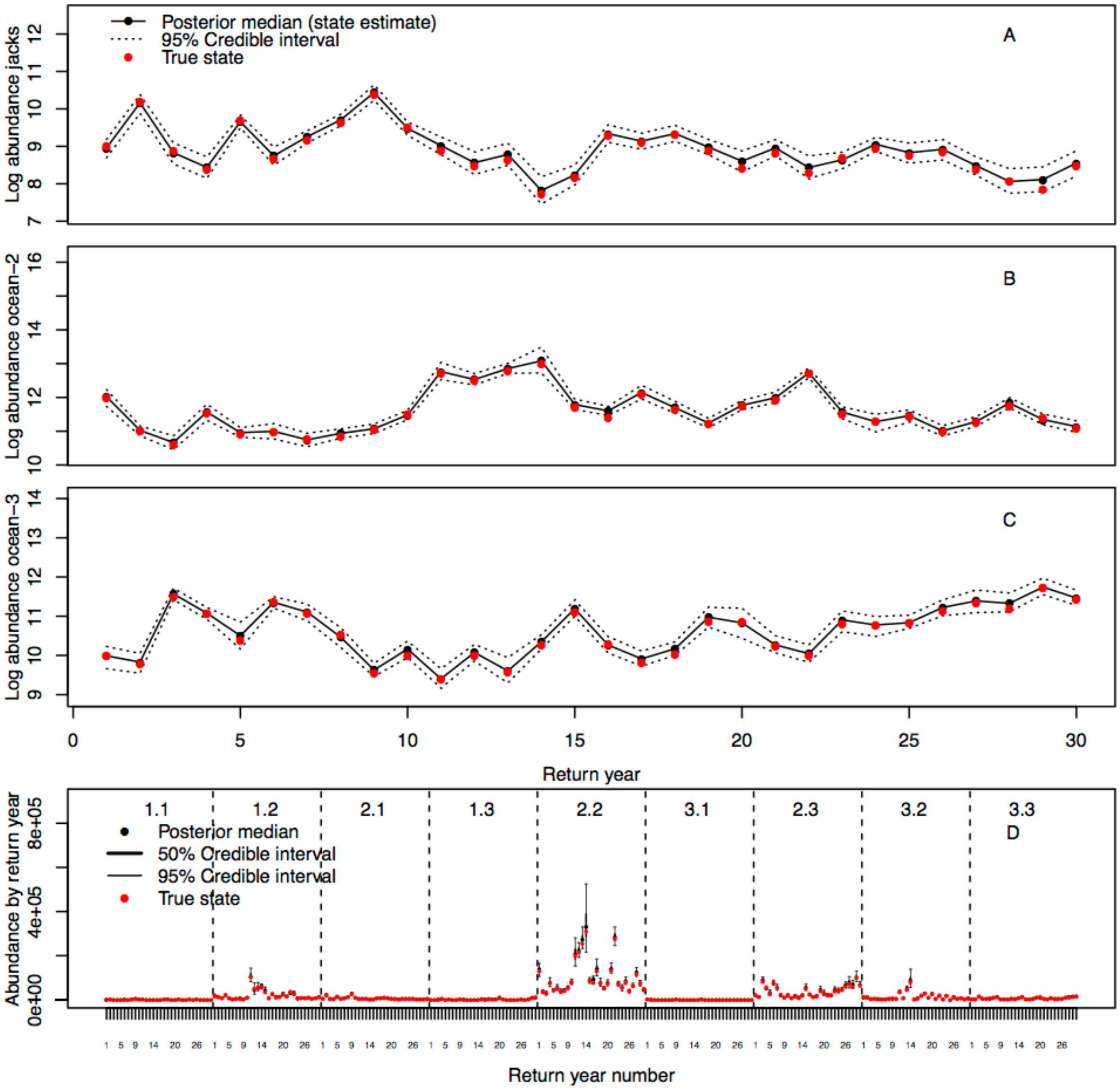


Figure B9. Model fit to simulated data for the univariate model of brood year jack proportions (eq. 2.2). Panel A depicts the credible intervals for estimated jack proportions relative to the true state values specified in the simulated data. Panel B depicts estimates for the coefficients of 5 covariates relative to the true values specified in the simulated data. Panel C depicts the credible intervals for estimated numbers-at age-by brood year relative to the values specified in the simulated data. Panels D and E depict the credible intervals for the model-predicted estimates of log abundance ($\ln\sum_{a=1}^{\omega} R_{t,a}^{s}$) relative to the values specified in the simulation for the harvest and escapement respectively. Panels F and G depict the credible intervals for the model-predicted estimates of age composition proportions ($\boldsymbol{\theta}_{t}^{s}$) over time relative to the values specified in the simulation for the escapement and harvest respectively.


Posterior median (state estimate)
95% Credible interval
True state
A
Log abundance jacks
7
8
9
10
11
12
B
Log abundance ocean−2
10
12
14
16
C
Log abundance ocean−3
9
10
11
12
13
14
0
5
10
15
20
25
30
Return year
1.1
1.2
2.1
1.3
2.2
3.1
2.3
3.2
3.3
D
Posterior median
50% Credible interval
95% Credible interval
True state
Abundance by return year
0e+00
4e+05
8e+05
1 5 9 14 20 26
Return year number

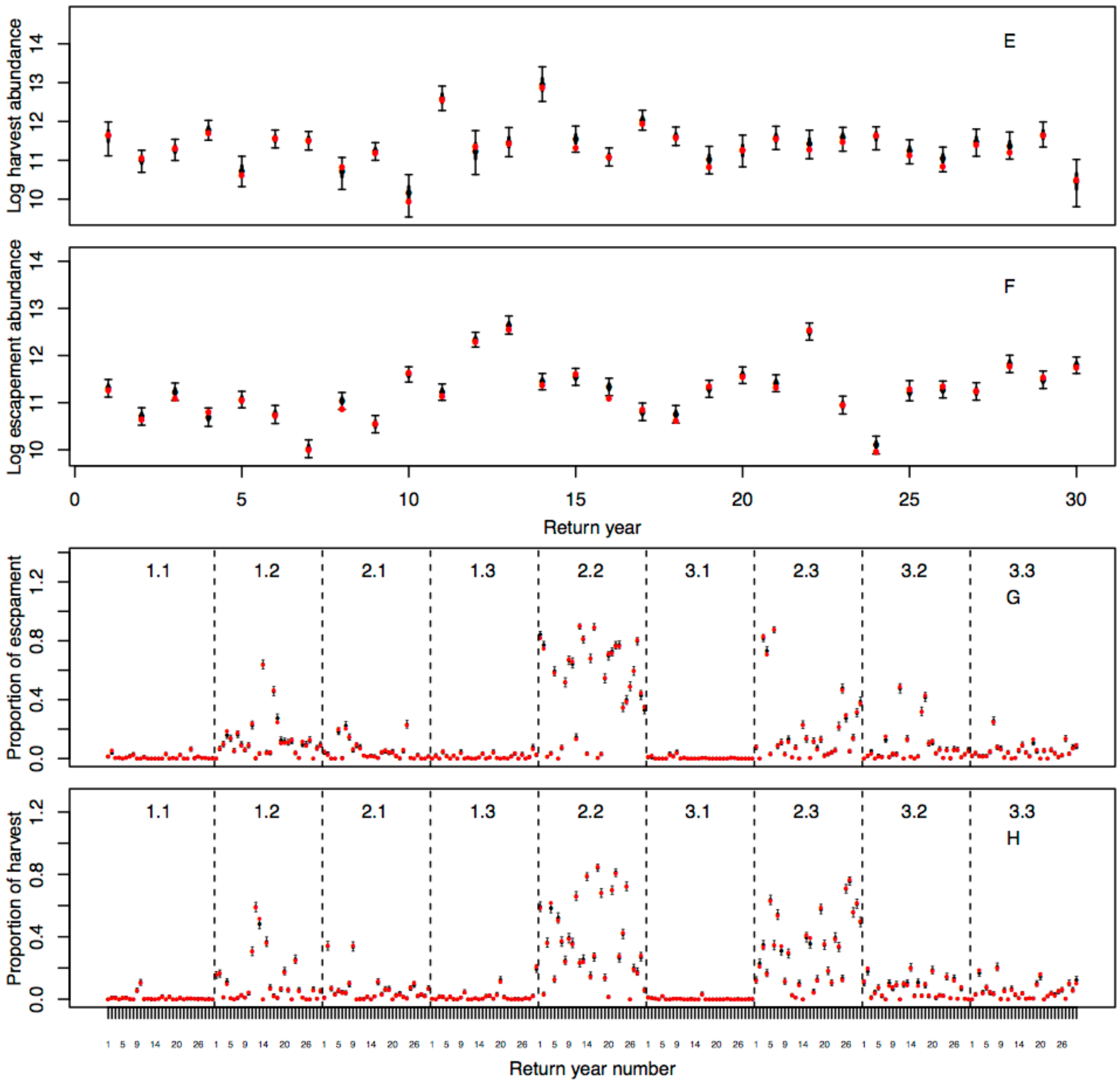
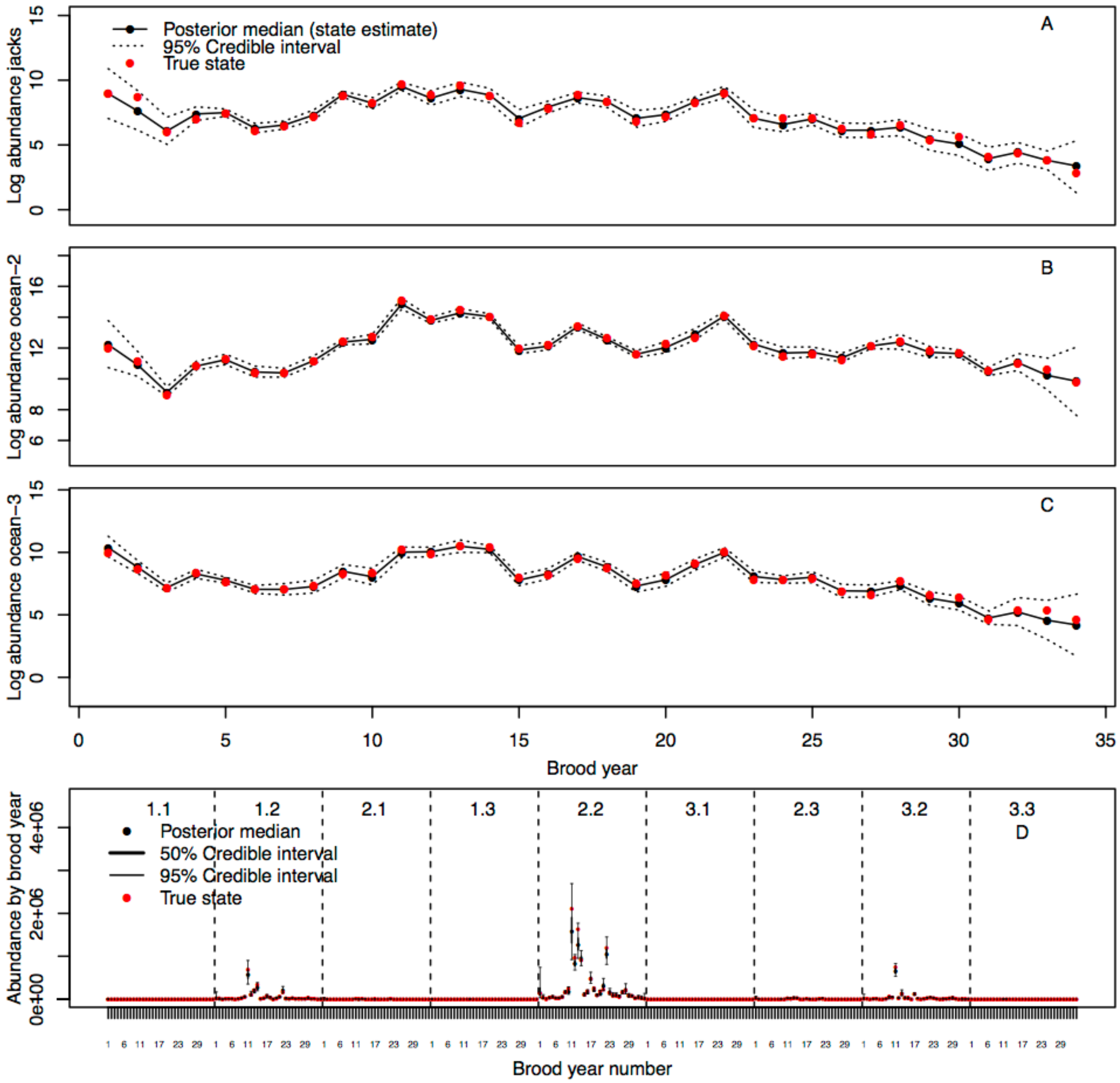


Figure B10. Model fit to simulated data for the multivariate model of return year abundance of ocean age classes (eq. 2.11). Panels A, B and C depict the credible intervals for state estimates of the return year log abundance of ocean age 1, 2, and 3 fish respectively relative to the values specified in the simulated data. Panel D depicts the credible intervals for estimated numbers-at-age by return year relative to the values specified in the simulated data. Panels E and F depict the credible intervals for the model-predicted state estimates of abundance ($\ln \sum_{a=1}^{\omega} R_{t,a}^{s}$) relative to the values specified in the simulation in the harvest and escapement respectively. Panels G and H depict the credible intervals for the model-predicted state estimates of age composition proportions ($\boldsymbol{\theta}_{t}^{s}$) over time relative to the values specified in the simulation in the escapement and harvest respectively.


A
Posterior median (state estimate)
95% Credible interval
True state
Log abundance jacks
B
Log abundance ocean-2
C
Log abundance ocean-3
Brood year
1.1
1.2
2.1
1.3
2.2
3.1
2.3
3.2
3.3
D
Posterior median
50% Credible interval
95% Credible interval
True state
Abundance by brood year
Brood year number

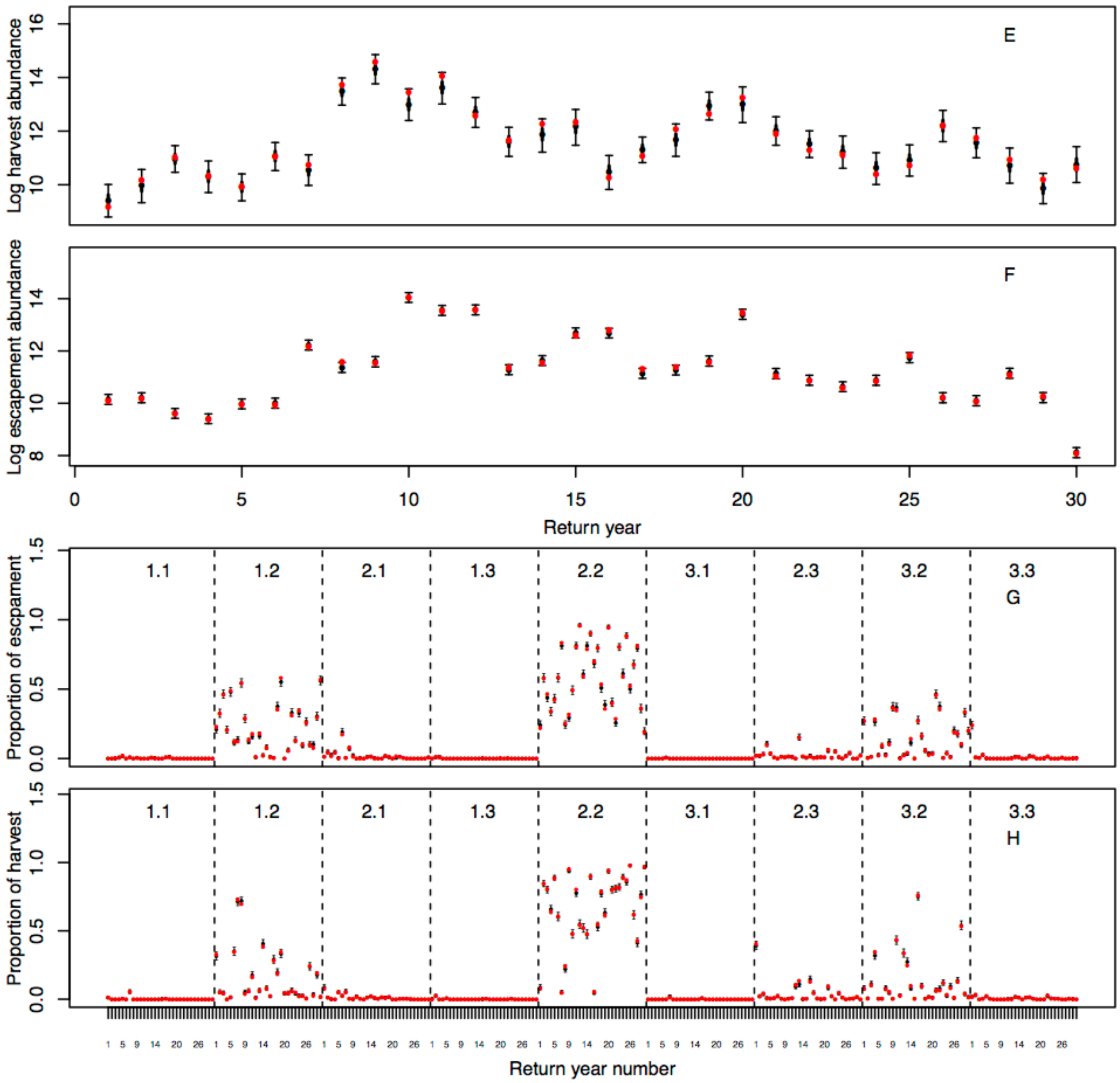


Figure B11. Model fit to simulated data for the multivariate model of brood year abundance of ocean age classes (eq. 2.10). Panels A, B and C depict the credible intervals for state estimates of the brood year log abundance of ocean age 1, 2, and 3 fish respectively relative to the values specified in the simulated data. Panel D depicts the credible intervals for estimated numbers at age by brood year relative to the values specified in the simulated data. Panels E and F depict the credible intervals for the model-predicted state estimates of abundance ($\ln\sum_{a=1}^{\omega} R_{t,a}^{s}$) relative to the values specified in the simulation in the harvest and escapement respectively. Panels G and H depict the credible intervals for the model-predicted state estimates of age composition proportions ($\boldsymbol{\theta}_{t}^{s}$) over time relative to the values specified in the simulation in the escapement and harvest respectively.

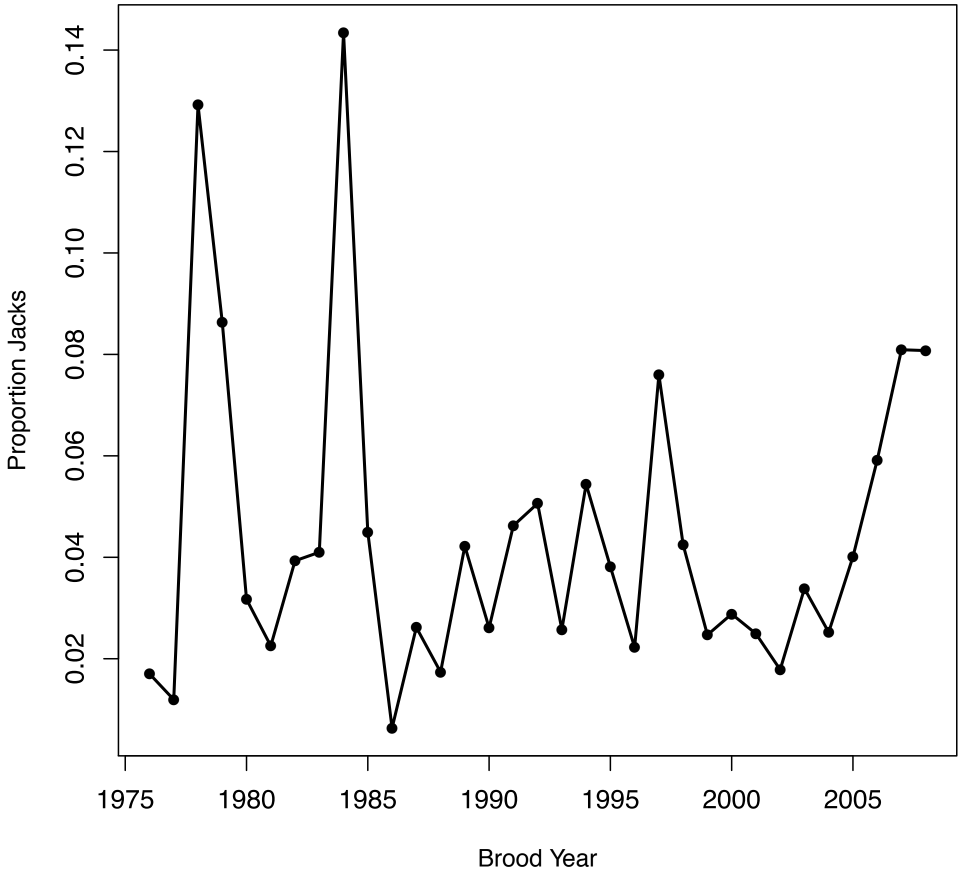


Figure B12. Jack proportions for the Ayakulik Sockeye salmon population by brood year over time.

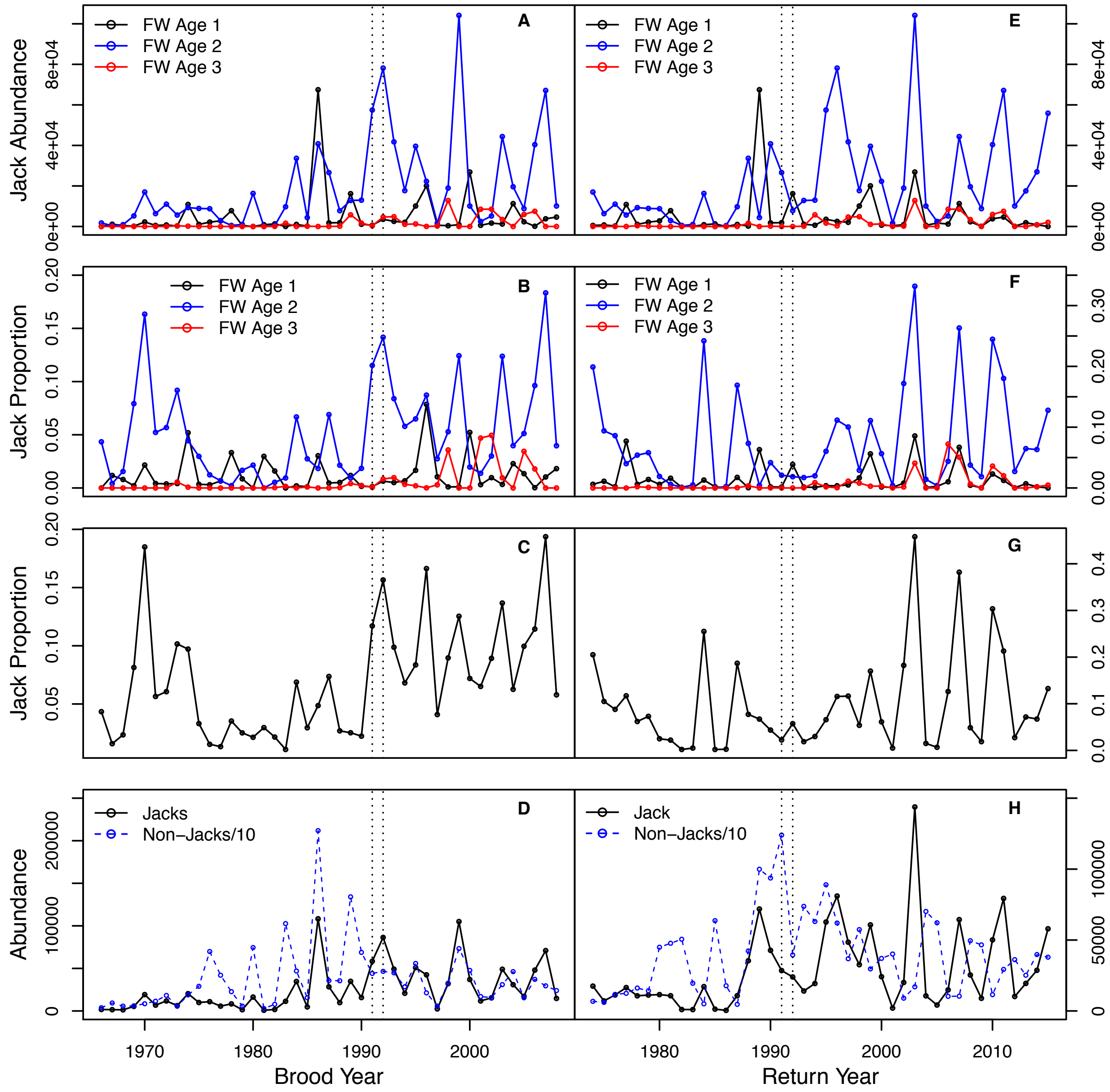


Figure B13. Age composition patterns over the full history of the Frazer Lake population (based on data from the ADF&G run reconstruction). Years 1991 and 1992 are indicated by vertical dotted lines. The 1991 run was dominated by ocean age-2 fish from the record-high 1986 recruitment, while most jacks spawning in this year were produced from the weaker 1987 cohort (Main text; Fig. 2.5B), leading to low jack proportions in that year's run (Main text; Fig. 2.5D). However, the 1987 cohort exhibited a relatively a high jack proportion (C). As such, although the

1991 run exhibited low jack proportions due to the numerical dominance of ocean age-2 fish, jacks were actually fairly abundant in this year's run (E). Importantly, 1991 was the first year in which the exploitation rate of jacks was substantially lower than that of older individuals (Main text; Fig. 2.6D) such that a large portion of the more abundant ocean age-2 and 3 fish were harvested, leaving a high proportion of jacks in the spawning escapement (Main text; Fig. 2.3A). Jacks were also a large portion of the spawners in 1992, partially due to continued higher exploitation rates on older fish in this year as well (Main text; Fig. 2.6D). Additionally, while most Frazer Lake sockeye mature at freshwater age-2, a large portion of jacks from the strong 1989 cohort spent only one year in freshwater for unknown reasons (A). These abundant three-year-old jacks returned to spawn in 1992, among ocean age-2 fish from the weak 1987 recruitment (Main text; Figure 2.6B).

APPENDIX C: CHAPTER 3

Table C1. List of model parameters, values used and sources (where available).

PARAMETER	DESCRIPTION	VALUE	UNIT	REFERENCE
L_∞^{ref}	Asymptotic average length (reference)	700	mm	Tuned
k^{ref}	Growth rate coefficient (reference)	0.25	year^{-1}	Tuned
$\rho_{L_\infty,k}$	Growth parameter trade-off	-0.0005	(mm*year)$^{-1}$	Ohlberger et al. 2019
σ_G	Variance in growth rate	0.1-0.3	year^{-1}	White et al. 2014
L_{juv}	Initial size at emergence	30	mm	Tuned
$\rho_{\gamma_0,k}$	Trait correlation (maturation and growth)	0.3	-	Ohlberger et al. 2019
α	Smolt productivity	60	Smolts/spawner	Worden et al. 2010
β	Smolt capacity	0.00017	-	Worden et al. 2010
σ_R	Recruitment variation	0.0-1.0	-	White et al. 2014, Thorson et al. 2014
$s_{a=3}$	Early marine survival (first year)	0.2	-	Farley et al., 2007
$s_{a>3}$	Late stage marine survival	0.8	-	Farley et al., 2007; Ruggerone, et al., 2003)
γ_0^{ref}	PMRN midpoint intercept	800	mm	Tuned, Kendall et al. 2014
λ	PMRN slope	-100	mm/yr	Tuned, Kendall et al. 2014
σ_{PMRN}	PMRN width	25	-	Tuned
ϑ	Mutation, segregation, recombination error	0.071	-	Enberg et al 2009
ϕ_k	Sex composition	0.5	-	NA
θ_{FDS}	Frequency-dependent slope	0-0.9	-	Ayalla and Capmbell 1973
μ	Frequency-dependent equilibrium	0.001-0.05	-	Sensitivity
u^{target}	Target exploitation rate	0.1-0.6	-	Sensitivity
σ_{catch}	Width of selectivity curve	0.1-2.0	-	Sensitivity
L_{max}	Fully selected body length	475	mm	Kendall, Hard, & Quinn, 2009

Table C2. List of sockeye salmon populations included in the empirical analysis, and the number of years of data available for each population and the source of the data (Department of Fisheries and Oceans (DFO), Canada, Alaska Department of Fish and Game (ADF&G).

REGION	POPULATION	YEARS	SOURCE
Fraser River	Birkenhead	62	DFO
	Bowron	62	DFO
	Chilko	62	DFO
	Scotch (Early)	30	DFO
	Stuart (Early)	62	DFO
	Fennell	43	DFO
	Gates	42	DFO
	Shuswap (Late)	62	DFO
	Stuart (Late)	61	DFO
	Nadina	37	DFO
	Portage	55	DFO
	Quesnel	62	DFO
	Raft	62	DFO
	Seymour	62	DFO
	Stellako	62	DFO
	Upper Pitt	62	DFO
	Weaver	44	DFO
	Harrison (omitted)		
Bristol Bay	Alagnak	44	ADF&G
	Egegik	44	ADF&G
	Igushik	44	ADF&G
	Kvichak	44	ADF&G
	Naknek	44	ADF&G
	Ugashik	44	ADF&G
	Wood	44	ADF&G
	Nushagak (omitted)		
Westward (AK)	Ayakulik (Red Lake)	32	ADF&G
	Black Lake	57	ADF&G
	Chignik Lake	57	ADF&G
	Frazer Lake	42	ADF&G
	Karluk (Early)	27	ADF&G
	Karluk (Late)	27	ADF&G
	Upper Station (Early)	39	ADF&G
	Upper Station (Late)	38	ADF&G

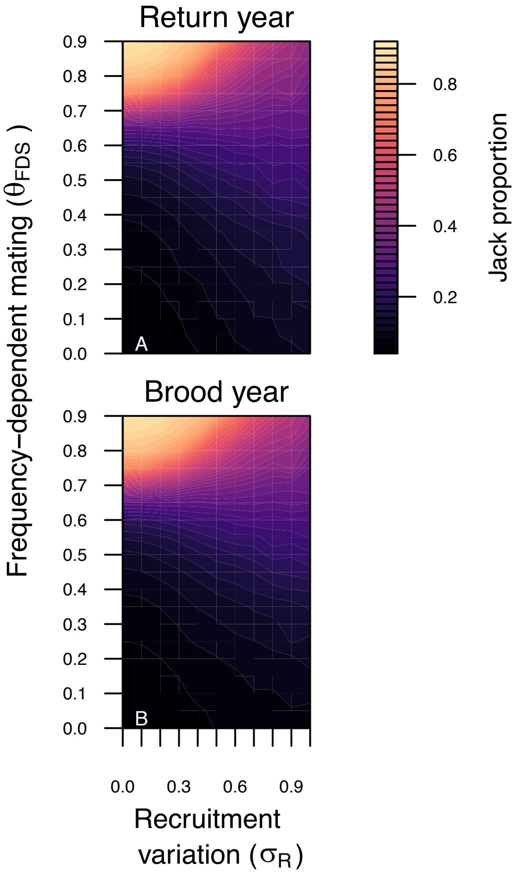


Figure C1. Contours of average population jack prevalence within cohorts (by brood year) in the final 200 years of the simulation across levels of recruitment variation (x axis, all panels), and magnitudes of negatively frequency-dependent reproductive success (y axis, all panels). Note that the y axis (θ_{FDS}) range extends to the full range of values considered (0.1-0.9) where in figures 3.2, C2-C3 it is truncated at 0.6.

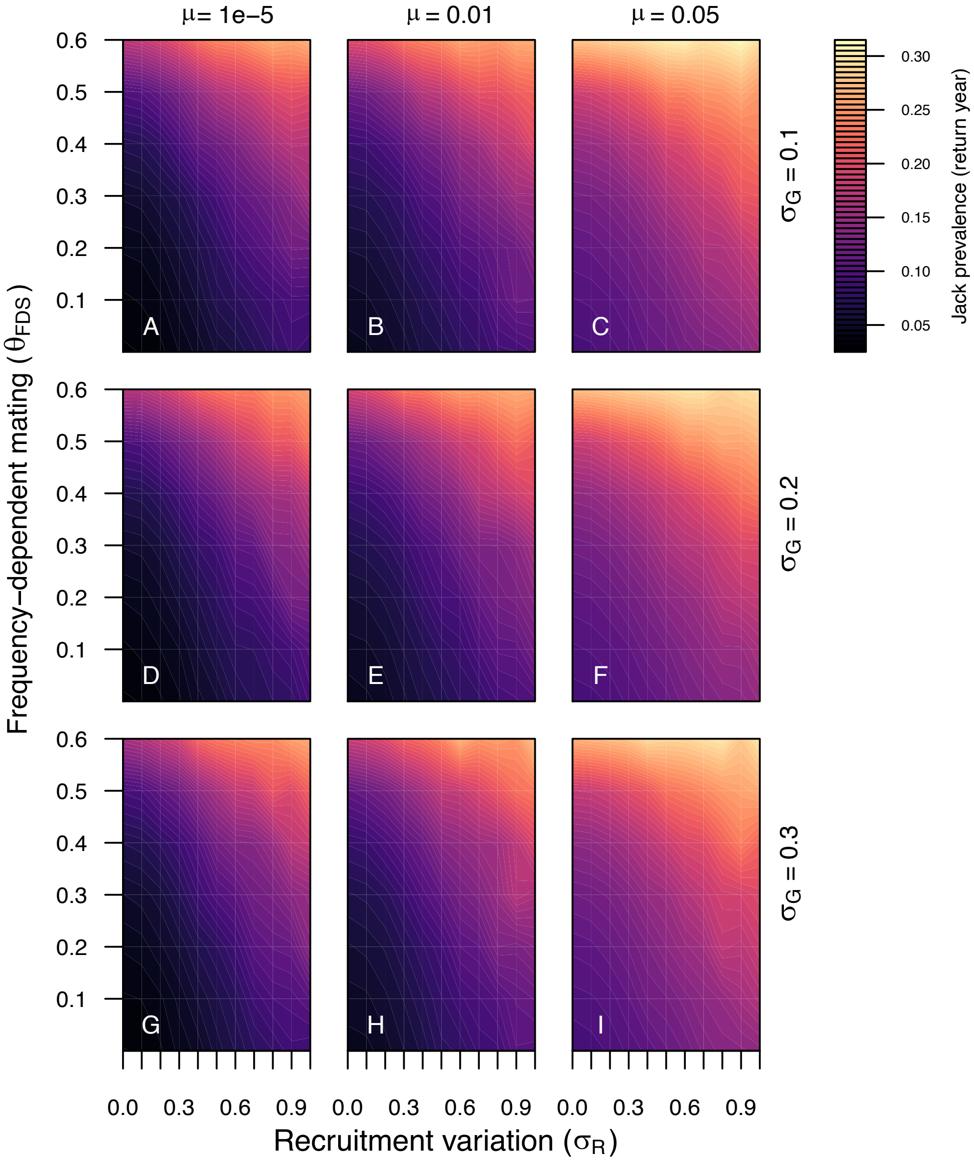


Figure C2. Contours of average jack prevalence within the breeding population prior to harvest (***by return year***) within the final 200 years of the simulation across levels of recruitment variation (x axis, all panels), and magnitudes of negatively frequency-dependent reproductive success (y axis, all panels). Each panel represents different values of growth variation (σ_G) and equilibrium jack:hooknose mating frequencies (μ) across simulations.

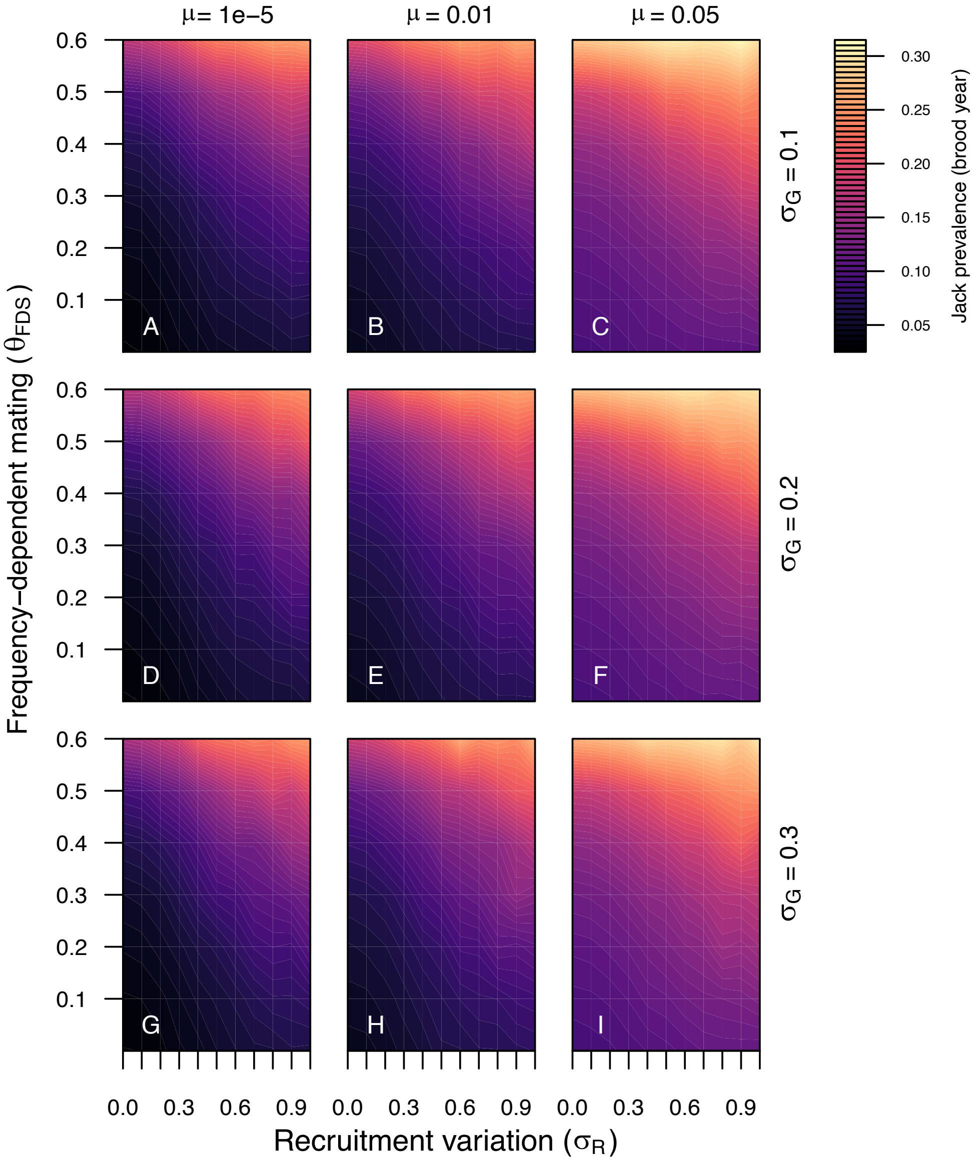


Figure C3. Contours of average jack prevalence within cohorts (***by brood year***) within the final 200 years of the simulation across levels of recruitment variation (x axis, all panels), and magnitudes of negatively frequency-dependent reproductive success (y axis, all panels). Each panel represents different values of growth variation (σ_G) and equilibrium jack:hooknose mating frequencies (μ) across simulations.

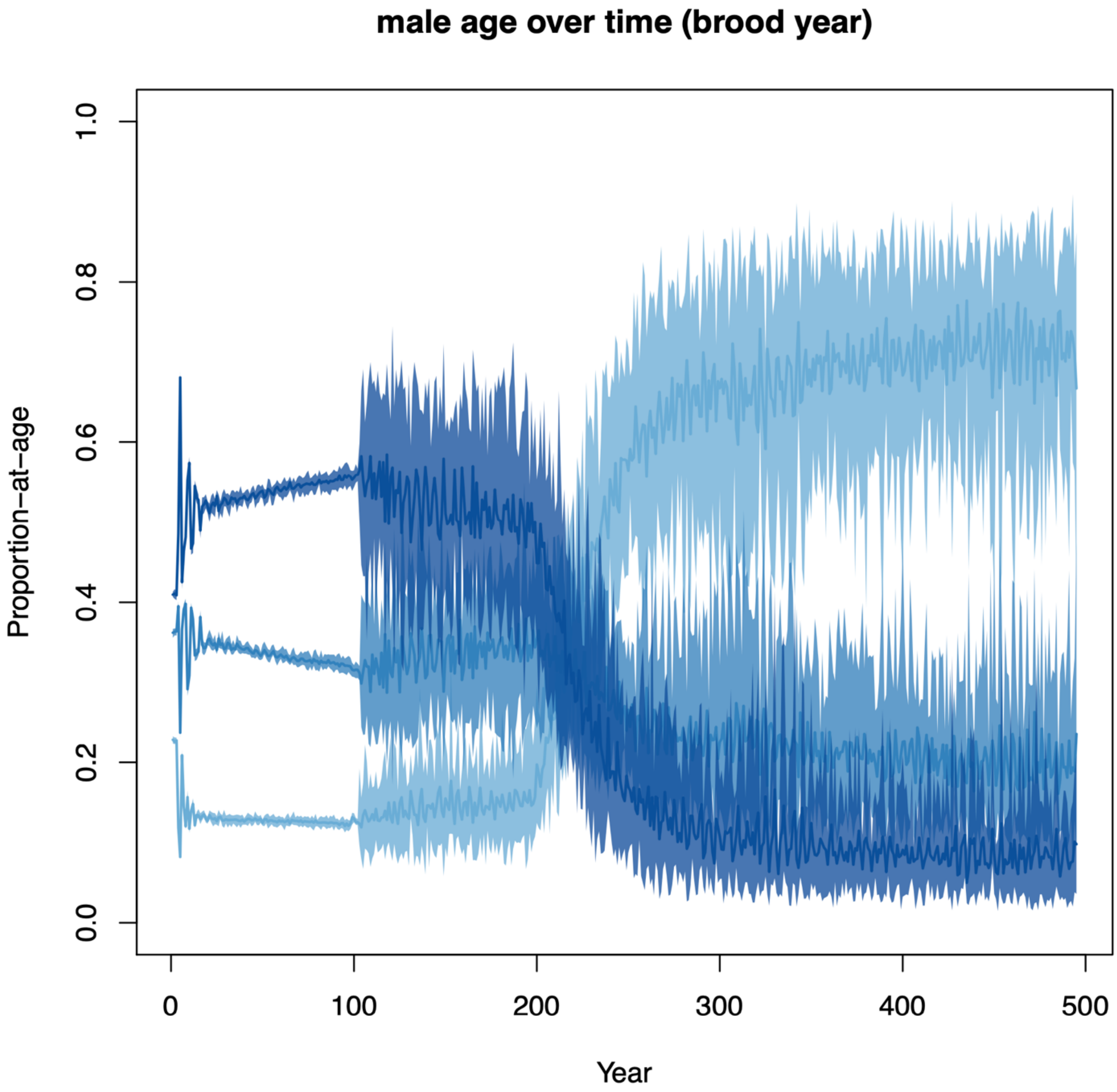


Figure C4. Example trajectory of changes in the age composition over time in response to size-selective harvest. Lines and shading the show the median and 95% intervals of the proportion of males maturing at ocean age -1 (light blue), ocean age-2 (intermediate blue) and ocean age-3 (dark blue). This time-series is for a fully selected exploitation rate of 0.6, and a value for σ_{catch} of 0.27, generating a highly size-selective vulnerability curve that largely excludes jacks.

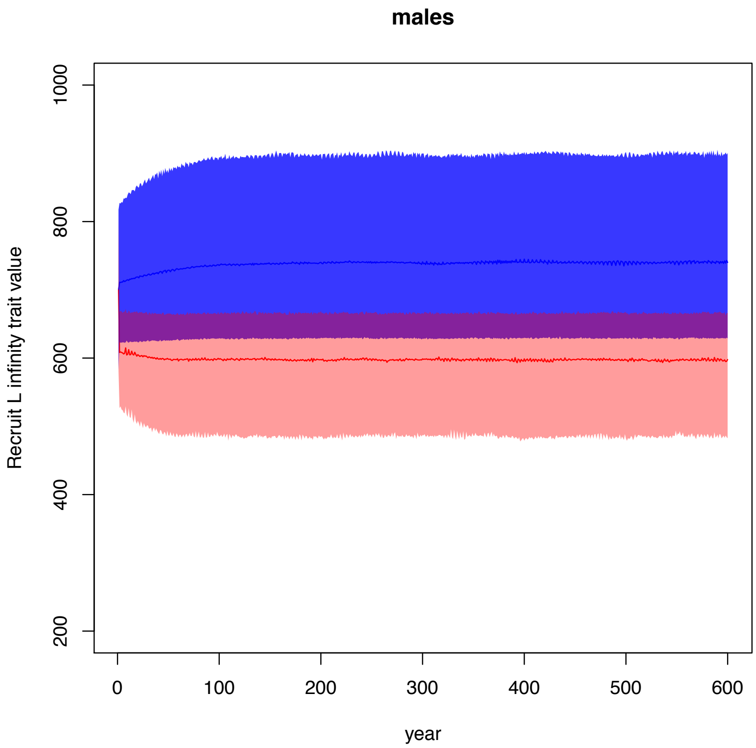


Figure C5. Example trajectory of trait evolution for male L_∞ values in the absence of recruitment variation.

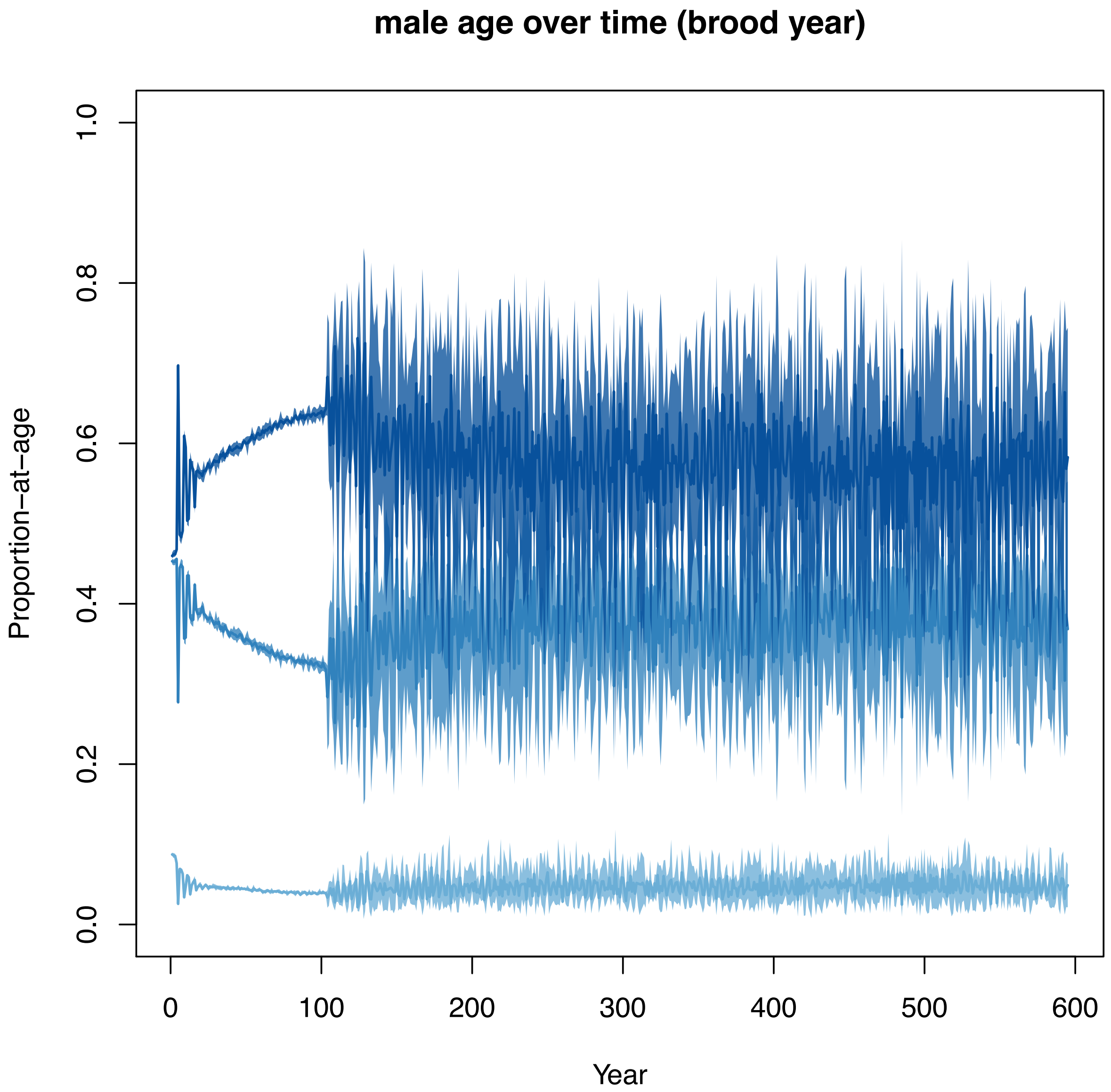


Figure C6. Example of simulated male age composition. Lines and shading the show the median and 95% intervals of the proportion of males maturing at ocean age -1 (light blue), ocean age-2 (intermediate blue) and ocean age-3 (dark blue). This time-series assumes a recruitment variation term of 0.5, growth variation of 0.1

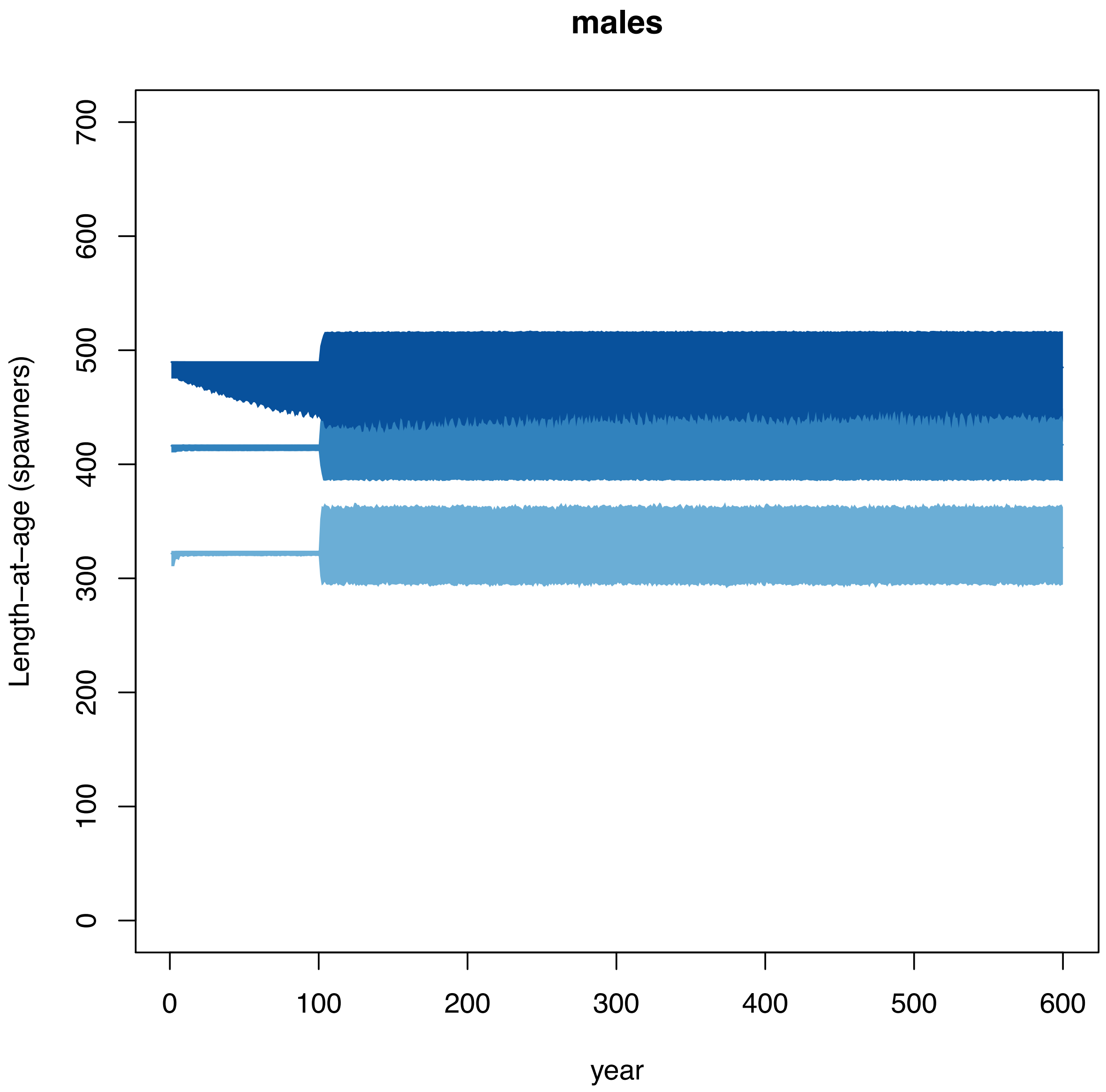


Figure C7. Example of male size-at-age distributions. Lines and shading the show the median and 95% intervals of the size-at-age of males maturing at ocean age -1 (light blue), ocean age-2 (intermediate blue) and ocean age-3 (dark blue). This time-series assumes a recruitment variation term of 0.5, growth variation of 0.1

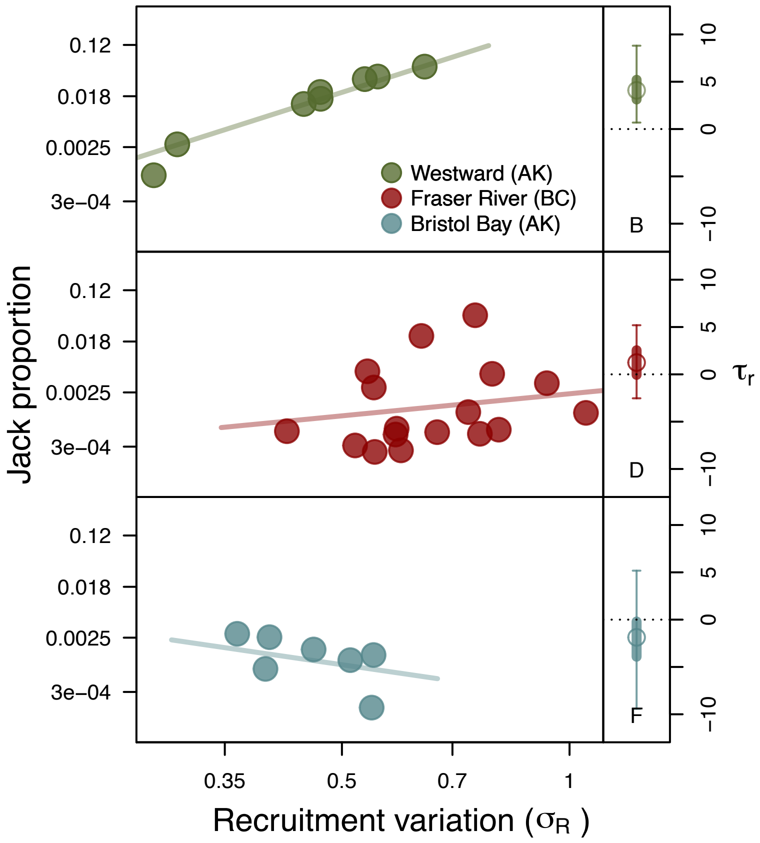


Figure C8. Estimated relationships between estimated population recruitment variability (σ_R) and jack prevalence by region assuming a Beverton-Holt stock-recruit relationship. All details of the figure are identical to those of figure 4.

Supplementary Methods: Initiation of the simulation model in year 1.

For the first year of the simulation, no information on spawner abundance exists to inform the first recruitment event. As such, the recruitment in year 1 is specified according to the asymptotic smolt recruitment of the Beverton-Holt equation:

$$(1) \quad N_{a=2,k,m=0}(t=1) = \frac{\alpha}{\beta}\phi_k$$

For subsequent age classes, abundance was calculated by projecting the number of recruits ($N_{a=2,k,m=0}(t=1)$) across the age distribution assuming the given survival probabilities:

$$(2) \quad N_{a>2,k,m=0}(t=1) = \left(1 - P_{a,k}(t=1)\right)S_{a-1}(t=1)N_{a-1,k,m=0}(t=1)$$

Growth is defined as a function of age as in eq. 2 (main text) and maturation probability is defined as a function of age and length (as in eq. 3 (main text)). This projection creates an initial age and size distribution, as well as set of mature individuals to serve as the spawning population for subsequent cohorts. It is assumed that there is no harvest in year 1.