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Stochastic recruitment alters the frequencies of alternative life histories in age-structured populations

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Abstract

Alternative reproductive tactics, where members of a population exhibit divergent mating approaches, are widespread in fishes. The maintenance of such polymorphisms is often explained using game-theoretic concepts such as frequency-dependent selection, which typically assume populations are at equilibrium. However, fish populations exhibit stochastic variability that is inconsistent with the assumption of equilibrium dynamics. We explored how stochastic population dynamics interact with sexual and harvest-induced selection to shape the frequencies of alternative male phenotypes in Pacific salmon (*Oncorhynchus* spp., Salmonidae). Males of several salmon species are composed of typical “hooknoses” that compete on the spawning grounds for mating opportunities, and rarer “jacks” that mature younger and at smaller sizes to attempt reproduction by “sneaking.” Using stochastic simulations, we found that realistic levels of recruitment variation could increase the prevalence of jacks relative to equilibrium expectations. This result is attributable to the “cohort mismatch” phenomenon, whereby differences in age at maturity between male phenotypes cause jacks from strong recruitments to spawn in the same year as hooknoses from weaker cohorts, elevating the proportion of jacks among spawners. Simulations were supported by data from major populations of sockeye salmon (*O. nerka*, Salmonidae) throughout their North American range, which indicated a positive association between recruitment variability and jack prevalence in some regions. Moreover, we found that frequency-dependent mating dampened population responses to fisheries-induced selection. Our findings emphasize that stochastic ecological processes are important to the maintenance of alternative life histories and interact with selection to produce emergent dynamics that have not previously been recognized.

KEYWORDS

alternative reproductive tactics, fisheries-induced evolution, frequency-dependent selection, salmon, simulation, sneaker male

1 | INTRODUCTION

Understanding how multiple discrete life-history pathways can co-exist within populations is an enduring puzzle in evolutionary ecology. Alternative phenotypes are widespread in fishes, including morphological polymorphisms (Hori, 1993), divergent male-mating

tactics (Taborsky, 2008) and partial migration (i.e. residents vs. migrants (Chapman et al., 2012)). The maintenance of such discontinuous trait variation is often explained using game-theoretic principles, whereby an individual's fitness varies based on the phenotypic expression of others in the 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 (Ayala & Campbell, 1974). 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 (Tomkins & Hazel, 2007)), yet predictions from each of these models implicitly assume a population at equilibrium, while fish stocks often vary stochastically across space and time. How stochastic population dynamics affect the evolution and maintenance of alternative life histories has received little consideration (but see Clark & Yoshimura, 1993; Kisdi & Meszén, 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; Taborsky et al., 2008). A common 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 that seek fertilizations through sneaking or subterfuge (“parasitic males”). ARTs are particularly common in teleost fishes (Taborsky, 2008), where they are often associated with variation in age-at-maturity and body size, and can influence a population's genetic diversity and age and size structure (Jones & Hutchings, 2002; Larsen et al., 2004; Rowe & 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, many fish stocks are also characterized by large and often unpredictable fluctuations in recruitment and abundance that violate the core assumptions of equilibrium population models (Hilborn & Walters, 1992). Therefore, equilibrium expectations from theoretical frameworks such as frequency-dependent selection may provide incomplete descriptions of the realized dynamics of ARTs in fish populations. Understanding how stochastic population dynamics interact with eco-evolutionary forces such as FDS may be important for the management of exploited fish stocks and offer insights into the evolution and maintenance of complex life histories under ecologically realistic scenarios.

Several species of Pacific salmon (*Oncorhynchus* spp.) 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 at an earlier age (Quinn, 2005). While generally ineffective at acquiring mates through courtship and intrasexual contests due to their small body

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sizes, jacks possess numerous specializations for achieving fertilizations through “sneaking,” including a higher gonadosomatic index, increased sperm velocity in river water (Flannery et al., 2013) and cryptic body colouration (Gross, 1984). Maturation age is heritable and sex-linked in salmonids (McKinney et al., 2019) such that males sired by jacks are more likely to become jacks themselves (Heath et al., 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 development (Thorpe, 1986). As such, both environmental and genetic factors can shape a male's developmental “decision” to become a jack (Heath et al., 2002; Vøllestad et al., 2004). Alternative life histories of male salmon are subject to FDS (Berejikian et al., 2010), such that their observed frequencies are expected to reflect an evolutionarily stable distribution of the proximate heritable traits underlying their expression (Gross, 1991; Hutchings & Myers, 1994). However, several studies have questioned whether such an equilibrium can realistically be achieved in the presence of persistent stochastic variation in recruitment (DeFilippo et al., 2019; Koseki & Fleming, 2006, 2007). Interannual variability in year-class strength combined with the difference in age-at-maturity between jack and hooknose males necessarily affects the ratio of male phenotypes present in the breeding population (Koseki & Fleming, 2006, 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 inflate the relative abundance of jacks in the breeding population (DeFilippo et al., 2019).

Here, we investigate how stochastic population dynamics interact with sexual and harvest-induced selection to shape the frequencies of alternative life histories. Using an individual-based simulation model that specifies interactions among population dynamics, life histories and reproductive behaviour, we find that levels of recruitment variation commonly observed in natural salmon 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 an important role of population dynamics in the maintenance of alternative phenotypes and suggest that non-equilibrium dynamics may be more important in shaping the realized behaviour of complex mating systems than is currently recognized.

2 | METHODS

2.1 | Individual-based model

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 (Figure 1). Our approach is similar to existing eco-evolutionary models (Enberg et al., 2009; Ohlberger et al., 2019), extended to represent the dynamics of alternative male phenotypes with frequency-dependent reproductive success. The simulation model was parameterized to represent a generic semelparous salmon population that included jack and hooknose male life histories. Individuals in this population were assumed to spend two years in freshwater and mature at ocean age 1 (total age, $a = 3$), ocean age 2 ($a = 4$) or ocean age 3 ($a = 5$). Jacks were defined as males maturing at ocean age 1 and hooknose males were those maturing at either ocean age 2 or ocean age 3.

Annual recruitment to the population was defined as the production of smolts (age two freshwater outmigrants) via a density-dependent Beverton-Holt function of the number of mature females in the breeding population ($N_F(t)$) (Figure 1a):

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

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

where $N_{a=2,k,m=0}(t)$ is the number of age two 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 $a < 3$ were 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 et al., 1998). In the Beverton-Holt function, α is the number of smolts produced per spawner at the limit of zero spawners, β controls the degree of density-dependence, and $\xi_R(t)$ are normally distributed recruitment deviations 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 was calculated as the product of total recruits and a sex composition term (ϕ_k), which was fixed at 0.5.

Each individual in the simulation (i) inherited three quantitative genetic traits that, in conjunction with stochastic environmental effects, determined its life-history trajectory: a growth rate coefficient (k) asymptotic adult length (L_∞), and an intercept of the probabilistic maturation reaction norm (γ_0) (PMRN; Heino et al., 2002). Given an individual's growth rate and asymptotic size, its length over time $L(i, t)$ followed a stochastic von-Bertalanffy function (Ohlberger et al., 2019; Figure 1b):

$$L(i, t) = L(i, t-1) + k(i) (L_\infty(i) - L(i, t-1)) e^{\xi_G(i, t)} \quad (2)$$

$$\xi_G(i, t) \sim \text{Normal}(-0.5\sigma_G^2, \sigma_G^2)$$

where, ξ_G is a normally distributed error term reflecting interannual variation in growth with a standard deviation of σ_G . While the von-Bertalanffy function can be problematic for modelling life-history evolution (Boukal et al., 2014), our analysis is narrowly concerned with the dynamic interplay between alternative male life histories rather than the determination of optimal growth and maturation trajectories. As such, we used the von-Bertalanffy as a mathematically convenient description of a typical growth curve (Czarnośki & Kozłowski, 1998).

Maturation was assumed to be a probabilistic function of individual length $L(i, t)$ and age $a(i, t)$ according to a PMRN with constant slope (λ) and width (σ_{PMRN}) (Table S1, Figure 1c):

$$p_{\text{mat}}(i, t) = \frac{1}{1 + e^{-\left(\frac{(L(i, t) - \gamma_0(i)) + \lambda a(i, t)}{\sigma_{\text{PMRN}}}\right)}} \quad (3)$$

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 (m) was stochastic and determined through a Bernoulli trial with a probability of $p_{\text{mat}}(i, t)$. This specification of maturation is advantageous in that it reflects the joint effects of an individual's genetics ($k(i), L_\infty(i), \gamma_0(i)$) and environmental conditions (σ_G) on the maturation decision. While maturing as a jack is heritable (Heath et al., 2002), it is also environmentally influenced (Vøllestad et al., 2004). This variation is thought to be related to growth, where under favourable growing conditions, more juveniles are likely to mature as jacks, regardless of their genotype, 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:

$$N_{a>2,k,m=0}(t) = (1 - P_{a,k}(t)) S_{a-1}(t) N_{a-1,k,m=0}(t-1) \quad (4)$$

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

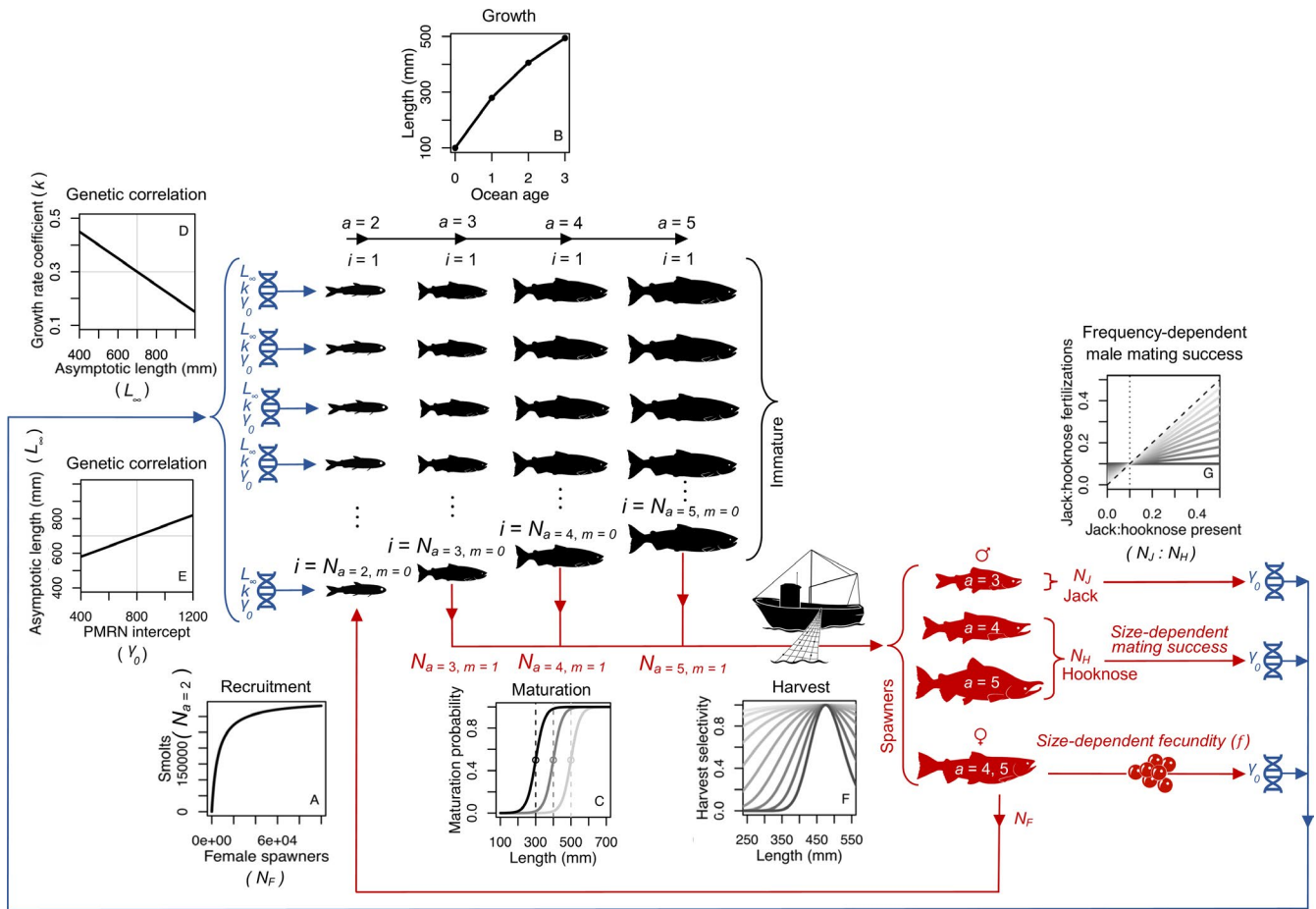


FIGURE 1 Simulation model functions and dynamics. Immature fish are shown in black, mature fish are shown in red, and genetic processes are shown in blue. Individuals (i) are added to the population as age 2 ($a = 2$) sexually immature ($m = 0$) smolts. The number of smolts produced each year ($N_{a=2,m=0}$) is determined by a Beverton-Holt function (Panel a) of female spawner abundance 2 years prior (N_F). Each year, surviving 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_∞). Individuals can reach maturity ($m = 1$) with a probability determined by their length, age, and 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 the 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 grey) to size-unselective (lighter grey) (f). Mature individuals that survive the fishery form the spawning escapement. Of the males in the escapement, the relative reproductive success of jacks ($a = 3$) vs. hooknose males ($a = 4, 5$) is determined by a linear negatively frequency-dependent mating function (Panel g). The dashed line in Panel (g) 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 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). Figure appears in colour in the online version only

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 was then specified as:

$$N_{a>2,k,m=1}(t) = P_{a,k}(t) S_{a-1}(t) N_{a-1,k,m=0}(t-1). \quad (5)$$

After mating, all mature individuals were removed from the population to represent the mortality associated with reproduction in semelparous salmon.

Of the females that reached maturity each year ($N_F(t)$), the expected share of the subsequent recruits produced by each individual $f(i_{k=1}, t)$ scaled exponentially with its length relative to the total lengths of all females in the population $\sum_{i_{k=1,m=1}=1}^{N_F(t)} L(i_{k=1,m=1}, t)$:

$$f(i_{k=1,m=1}, t) = \frac{L(i_{k=1,m=1}, t)^\varphi}{\sum_{i_{k=1,m=1}=1}^{N_F(t)} L(i_{k=1,m=1}, t)^\varphi} N_{a=2}(t+2) \quad (6)$$

where $N_{a=2}(t+2)$ is the total number of recruits produced by the year t breeding event according to the Beverton-Holt function and φ is the fecundity exponent (McGurk, 2000). The number of smolts produced by each female was multinomially distributed, with a set of probabilities equal to the relative fecundities of all females in the breeding population $f(i)$, and a number of trials equal to the number of recruits ($N_{a=2}(t+2)$).

Each female probabilistically selected a male to sire her offspring. 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 (Figure 1g):

$$\frac{E_J(t)}{E_H(t)} = \begin{cases} \mu(1 - \theta_{FDS}) + \theta_{FDS} \left(\frac{N_J(t)}{N_H(t)} \right), & N_J(t) > 0 \\ 0, & N_J(t) = 0 \end{cases} \quad (7)$$

where:

$$N_J(t) = N_{a=3,k=2,m=1}(t) \quad (8)$$

and

$$N_H(t) = \sum_{a=4}^5 N_{a,k=2,m=1}(t). \quad (9)$$

Here, $\frac{E_J(t)}{E_H(t)}$ is the ratio of eggs sired by jack males ($E_J(t)$) relative to eggs sired by hooknose males ($E_H(t)$), 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 mating function crosses the 1:1 line). We assumed that the shape of the frequency-dependent mating function arises from qualities of the spawning habitat (DeFilippo et al., 2018; Gross, 1991) and thus is invariant over time and equivalent among the entire population (but see Young, 1999).

The proportion of a given cohort sired by jacks $\psi(t)$ was then calculated as:

$$\psi(t) = \frac{\frac{E_J(t)}{E_H(t)}}{\frac{E_J(t)}{E_H(t)} + 1} = \frac{E_J(t)}{E_J(t) + E_H(t)}. \quad (10)$$

For each individual jack, its probability of siring a female's offspring ($\pi(i_{a=3,k=2,m=1}, t)$) was then equal to the total proportion of offspring sired by jacks that year ($\psi(t)$) relative to the total number of jacks present:

$$\pi(i_{a=3,k=2,m=1}, t) = \frac{\psi(t)}{N_J(t)} \quad (11)$$

Similarly, an individual hooknose male's probability of mating depended on the total proportion of offspring sired by hooknose males collectively 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 ($\pi(i_{a>3,k=2,m=1}, t)$) was assumed to be directly proportional to its relative length:

$$\pi(i_{a>3,k=2,m=1}, t) = \frac{1 - \psi(t)}{N_H(t)} \frac{L(i_{a>3,k=2,m=1}, t)}{\sum_{i_{a>3,k=2,m=1}=1}^{N_H(t)} L(i_{a>3,k=2,m=1}, t)} \quad (12)$$

There is a growing body of evidence that age-at-maturity (McKinney et al., 2019) and male reproductive tactics specifically (Heath et al., 2002) follow sex-linked inheritance in salmon. Restricted recombination between the sex chromosomes allows for alleles associated with early maturation to exist within a population that does not confer early maturation to females, for which this trait would be deleterious. Such sex-specific genetic architecture underlying age-at-maturity is likely important to the evolution and maintenance of alternative male life histories in salmon populations (McKinney et al., 2021). As a simplified representation of this system of inheritance, males and females in our simulation inherited trait values from their father and mother respectively rather than a mix of both parents. For simplicity, we assumed that the primary trait passed down to an individual's offspring was the intercept of the PMRN (γ_0 , Eq. 3):

$$\gamma_0(o_k) \sim \text{Normal}(\gamma_0(i_k), \vartheta \gamma_{0,\text{ref}}) \quad (13)$$

where $\gamma_0(o_k)$ 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, $\gamma_{0,\text{ref}}$ 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 (Enberg et al., 2009). The evolutionary dynamics were assumed to be driven by the intercept of the PMRN because available evidence suggests that evolution is more likely to shift the intercept rather than the slope (Eikeset et al., 2016).

Values for offspring growth parameters were 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 ($\rho_{\gamma_0, L_\infty}$), such that individuals with a lower intercept of the PMRN matured younger and thus reached a smaller final body size (Figure 1e), as is expected for semelparous species:

$$L_\infty(i) = L_{\infty,\text{ref}} + \rho_{\gamma_0, L_\infty} (\gamma_0(i) - \gamma_{0,\text{ref}}) \quad (14)$$

Similarly, we assumed that growth rate and asymptotic size were negatively correlated ($\rho_{L_\infty, k}$, Figure 1d) (Beverton, 1992; Helser & Lai, 2004; Pilling et al., 2002).

$$k(i) = k_{\text{ref}} + \rho_{L_\infty, k} (L_\infty(i) - L_{\infty,\text{ref}}) \quad (15)$$

where k_{ref} and $L_{\infty,\text{ref}}$ are the reference values for growth rate and asymptotic size respectively. As such, individuals that grew more slowly were expected to take longer to mature and ultimately reach a larger size. Relaxing the assumed correlations between the PMRN intercept, asymptotic length, and growth rate did not qualitatively alter model outcomes (Figure S1).

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 rate (F):

$$F = -\log(1 - u_{\text{target}}). \quad (16)$$

Each mature individual was then assigned a probability of being harvested $\rho(i)$ that was determined by the target fishing mortality rate and the individual's body size:

$$\rho(i_{m=1}, t) = 1 - e^{-Fv(i_{m=1})} \quad (17)$$

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

$$v(i_{m=1}) = e^{\frac{-(\log(L(i_{m=1}, t)) - \log(L_{\text{max}}))^2}{2\sigma_{\text{catch}}^2}} \quad (18)$$

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 (Table S1) and σ_{catch} determines the width of the curve (Ohlberger et al., 2019) (Figure 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 was harvested (H) was then determined through a Bernoulli trial with a probability of $p_{\text{catch}}(i)$. Because the realized exploitation rate (u_{real}) could differ from the target depending on the shape of the selectivity curve relative to the size structure of the population, the realized harvest rate was calculated as the total number of individuals harvested divided by the total number of individuals that matured that year ($N_R(t)$):

$$u_{\text{real}} = \frac{\sum_{i=1}^{N_R(t)} \text{Bernoulli}(p_{\text{catch}}(i_{m=1}, t))}{N_R(t)} \quad (19)$$

where:

$$N_R(t) = \sum_{a=3}^5 \sum_{k=1}^2 N_{a,k,m=1}(t). \quad (20)$$

While the difference between target and realized exploitation rates depends on the degree of harvest size selectivity, the age and size composition of the population, and the level of fishing mortality, we note that the range of u_{real} values was generally within the range of specified values of u_{target} .

2.2 | Model simulations

In the first year of the simulations, the number of recruits was set to the asymptotic smolt recruitment (α/β), and PMRN intercept values of all individuals were randomly drawn from a normal distribution

with mean $\gamma_{0,\text{eff}}$ and a standard deviation of 200. The initial age and size structure of the population was set by projecting the asymptotic smolt recruitment through each age class and applying the growth function and survival and maturation probabilities. Stochastic simulations were run for 1,000 years, with the first 750 treated as a "burn-in" period. In harvest simulations, fishing was initiated after the first 500 years. Population dynamics were simulated over a range of values for recruitment variability ($\sigma_R = 0.0 - 1.0$ (Thorson et al., 2014; White et al., 2014)), as well as variation in growth ($\sigma_G = 0.1 - 0.3$ (Figure S2-S3); (Ohlberger et al., 2019; 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, Figure 1g), and we explored scenarios across a range of equilibrium mating frequencies ($\mu = 0.0001, 0.01, 0.05$, Figure S2-S3). 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 unselective (Figure 1f). Full details of the model's parameterization can be found in Table S1. In all simulations, we monitored the prevalence of jacks (ocean age 1/total age 3 males) within cohorts (by brood year), and in the breeding population prior to harvest (by return year). The proportion 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). Example trajectories of demographic and life-history parameters over time can be found in Figures S4-S7.

2.3 | Empirical analysis

To empirically evaluate the relationship between jack prevalence and recruitment variation in natural populations, we examined long-term monitoring data from wild sockeye salmon (*O. nerka*) throughout their North American range. We included data from the Fraser River in British Columbia (17 stocks), Bristol Bay, Alaska (7 stocks), and the Westward region of Alaska (Alaska Peninsula and Kodiak Archipelago) (8 stocks) (Table S2). We focus on sockeye salmon here due to the relatively large number of wild populations of this species that are not subject to hatchery influences and have long time-series of high-quality age composition and spawner-recruit data available. Due to the well-established effects that hatchery propagation can have on jack prevalence (Hankin et al., 2009; Unwin & Glova, 1997) we avoided data from hatchery-influenced stocks.

Recruitment variation for each population was estimated using a Bayesian hierarchical Ricker stock-recruit model (Ricker, 1954):

$$\log(R_{p,y}) = \log(S_{p,y}) + \log(\alpha_p) - \beta_p S_{p,y} + \omega_{p,y} \quad (21)$$

where α_p and β_p are the productivity and (inverse) capacity terms for population p , $R_{p,y}$ is the number of adult recruits to population p in brood year y that resulted from the escapement in that year ($S_{p,y}$), and $\omega_{p,y}$ are the recruitment residuals. 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 deviations from the stock-recruit relationship into autocorrelated and independent error components (Fleischman et al., 2013) where ϕ is the AR lag-1 coefficient of the previous year's model residual $\omega_{p,y}$ such that:

$$\omega_{p,y} = \phi \omega_{p,y-1} + \varepsilon_{p,y} \quad (22)$$

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

$$\varepsilon_{p,y} \sim \text{Normal}(0, \sigma_{R_p}). \quad (23)$$

The analysis described here was also repeated using a Beverton-Holt spawner-recruit function (Figure S8). Productivity parameters were modelled hierarchically among populations using a non-centered parameterization (Betancourt, 2016):

$$\log(\alpha_p) = \mu_\alpha + \sigma_\alpha Z_{a_p} \quad (24)$$

where μ_α is the among-population mean productivity, σ_α is the standard deviation, and Z_{a_p} is a standard scaling factor that follows a normal distribution with a mean of zero and a standard deviation of one (Betancourt, 2016). Because the capacity terms (β_p) are not transportable between populations (Hilborn & Liermann, 1998), these parameters were specified independently for each stock.

Recruitment variation terms (σ_{R_p}) were also modelled hierarchically among populations in the same form as Equation 24. The estimated recruitment variation term for each population (σ_{R_p}) was then related to its jack prevalence according to:

$$\zeta_{p,y} = L_p \quad (25)$$

$$L_p \sim \text{Normal}(\mu_{L_p}, \sigma_{L_p|p \in Q_r}) \quad (26)$$

$$\mu_{L_p} = \mu_{r|p \in Q_r} + \tau_{r|p \in Q_r} \sigma_{R_p} \quad (27)$$

where $\zeta_{p,y}$ is the predicted logit jack proportion in population p in year y , and L_p is a random effect describing that population's jack prevalence with a mean (μ_L) defined by a linear relationship with the population's recruitment variability (σ_{R_p}). The intercept ($\mu_{r|p \in Q_r}$) and slope ($\tau_{r|p \in Q_r}$) of the linear function, and the residual population-level variation in jack prevalence ($\sigma_{L_p|p \in Q_r}$) varied by region, where Q_r represents the set of populations belonging to region r , and $r|p \in Q_r$ denotes the region to which population p belongs (e.g. Bristol Bay, Fraser, Westward AK).

Recruit abundance was assumed to follow a lognormal likelihood:

$$E_{p,y} \sim \text{Lognormal}(\log(R_{p,y}), \sigma_{\text{obs}}) \quad (28)$$

where $E_{p,y}$ are the observed adult recruits for population p and year y , and σ_{obs} is the lognormal observation error term for these data which

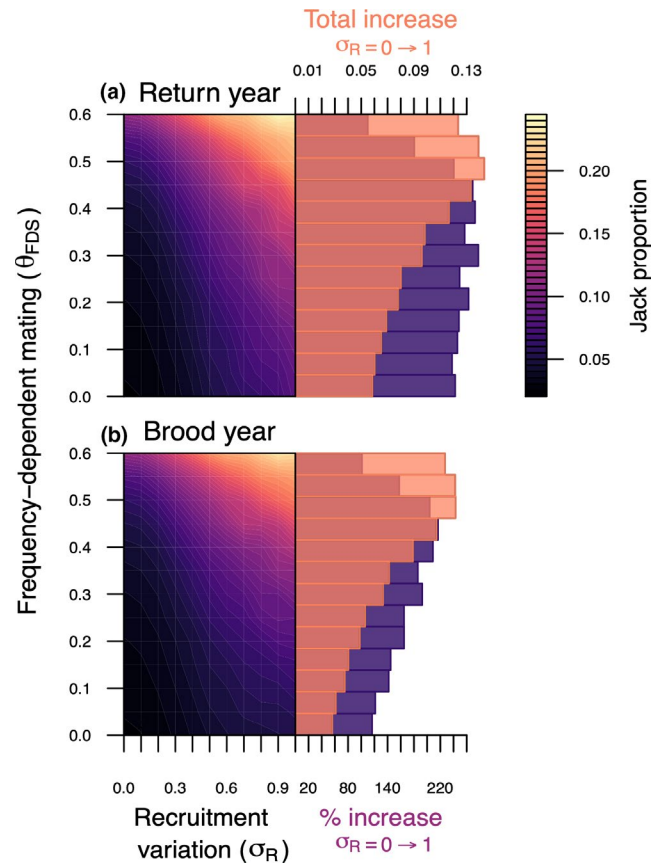


FIGURE 2 Contours of average jack prevalence across levels of recruitment variation and frequency-dependent mating. Panels show jack prevalence by return year (Panel a), and by brood year (Panel b) in the final 250 years of the simulation across levels of recruitment variation ($\sigma_R = 0.0$ – 1.0) 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 at equilibrium ($\theta_{FDS} \leq 0.6$). Results shown here are for intermediate values of growth variation ($\sigma_G = 0.2$) and equilibrium mating frequencies ($\mu = 0.01$). Adjoining histograms show the relative (purple) and absolute (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 appears in colour in the online version only

was fixed at 0.5. Spawner abundance ($S_{p,y}$) was assumed to be observed without error, although specifying observation noise in these data across a range of feasible values did not qualitatively affect model results (Figure S9–S10). Logit observed jack proportions ($\text{Logit}(J_{p,y})$) were assumed to be normally distributed around the estimated values ($\zeta_{p,y}$) with region-specific observation error terms ($\sigma_{J_{p,y}|p \in Q_r}$) which were freely estimated:

$$\text{Logit}(J_{p,y}) \sim \text{Normal}(\zeta_{p,y}, \sigma_{J_{p,y}|p \in Q_r}). \quad (29)$$

A complete glossary of model terms and associated prior distributions can be found in Table S3.

FIGURE 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 level of harvest selectivity (σ_{catch}) re-calculated from specified target exploitation rates from 0.1 to 0.6. The colour of the dots represents the different levels of frequency-dependent mating that were considered (θ_{FDS}). Panels (a–c) show the results for levels of recruitment variation (σ_R) of 0.4, 0.6, and 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 $L_{\infty \text{ref}} = 700$ and $k_{\text{ref}} = 0.3$. Solid lines represent median values, and transparent boundaries show the 25th and 75th quantiles of the size distribution of each age class according to the degree of growth variation assumed in these simulations ($\sigma_G = 0.2$). Figure appears in colour in the online version only

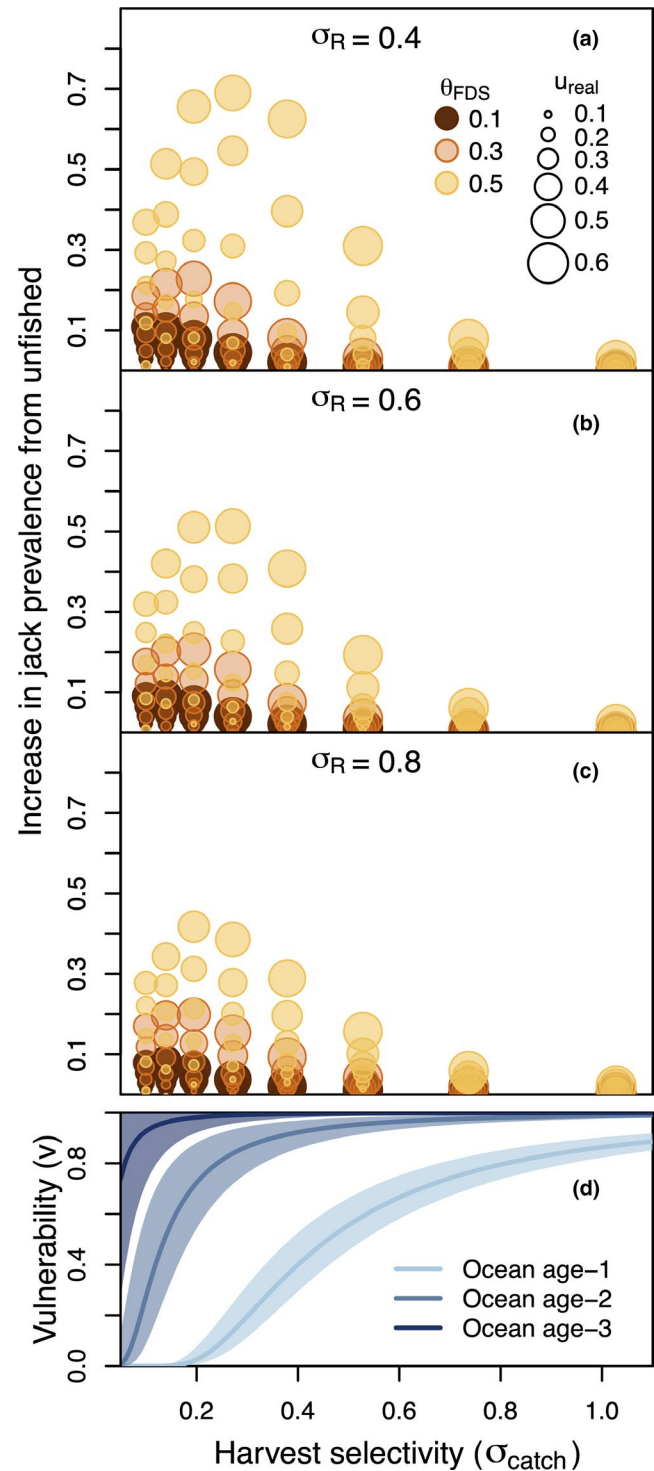
3 | RESULTS

3.1 | Demographic simulations

The prevalence of jacks was highly variable across dimensions of both frequency-dependence (θ_{FDS}) and recruitment variation (σ_R). When negative frequency-dependent mating success was strongest (i.e. $\theta_{\text{FDS}} = 0$ –0.2), jacks were maintained at low levels ($\leq 5\%$ of males, Figure 2). Conversely, when the strength of negative frequency-dependent mating was relaxed ($\theta_{\text{FDS}} = 0.7$ –0.9), as much as 50%–100% of males in the population matured as jacks (Figure S11). At all values of frequency-dependence that did not result in a majority of males maturing as jacks at equilibrium ($\theta_{\text{FDS}} = 0$ –0.6), the jack prevalence of the population increased with greater recruitment variation (Figure 2). For instance, at $\theta_{\text{FDS}} = 0.5$, the equilibrium ($\sigma_R = 0$) proportion of males maturing as jacks within cohorts (by brood year) was 0.06, which increased to 0.09 at $\sigma_R = 0.3$, 0.13 at $\sigma_R = 0.6$, and 0.18 at $\sigma_R = 1.0$, an increase of 200% (Figure 2b). Recruitment variation had an even larger effect on the prevalence of jacks in the breeding population (by return year), elevating it by over 270% in certain parameter regions (Figure 2a). The effect of recruitment variation on the population's jack proportions was not uniform across levels of frequency dependence. For instance, when θ_{FDS} was relaxed such that $\geq 50\%$ of males in the population matured as jacks ($\theta_{\text{FDS}} = 0.7$ –0.9), increasing recruitment variation decreased the levels of jacks in the population (Figure S11). At the strongest levels of frequency-dependence $\theta_{\text{FDS}} = 0$ –0.2, recruitment variation increased the proportion of individuals maturing as jacks, but the effect was smaller compared to intermediate levels of FDS ($\theta_{\text{FDS}} = 0.3$ –0.5) (Figure 2).

3.2 | Harvest simulations

Fishing had little effect on the proportion of males maturing as jacks when vulnerability to harvest was unrelated to body size (Figure 3).



Conversely, when harvest selected for larger individuals, fishing could increase jack prevalence substantially compared to an unfished population in the same parameter space (Figure 3). However, the effects of size-selective harvest depended 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 (Figure 3). Alternatively, when frequency-dependent mating was relaxed ($\theta_{\text{FDS}} = 0.5$) size-selective fishing could increase jack proportions substantially. The effects of harvest

were generally 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 on jack prevalence (compare Figure 3a–c).

3.3 | Empirical results

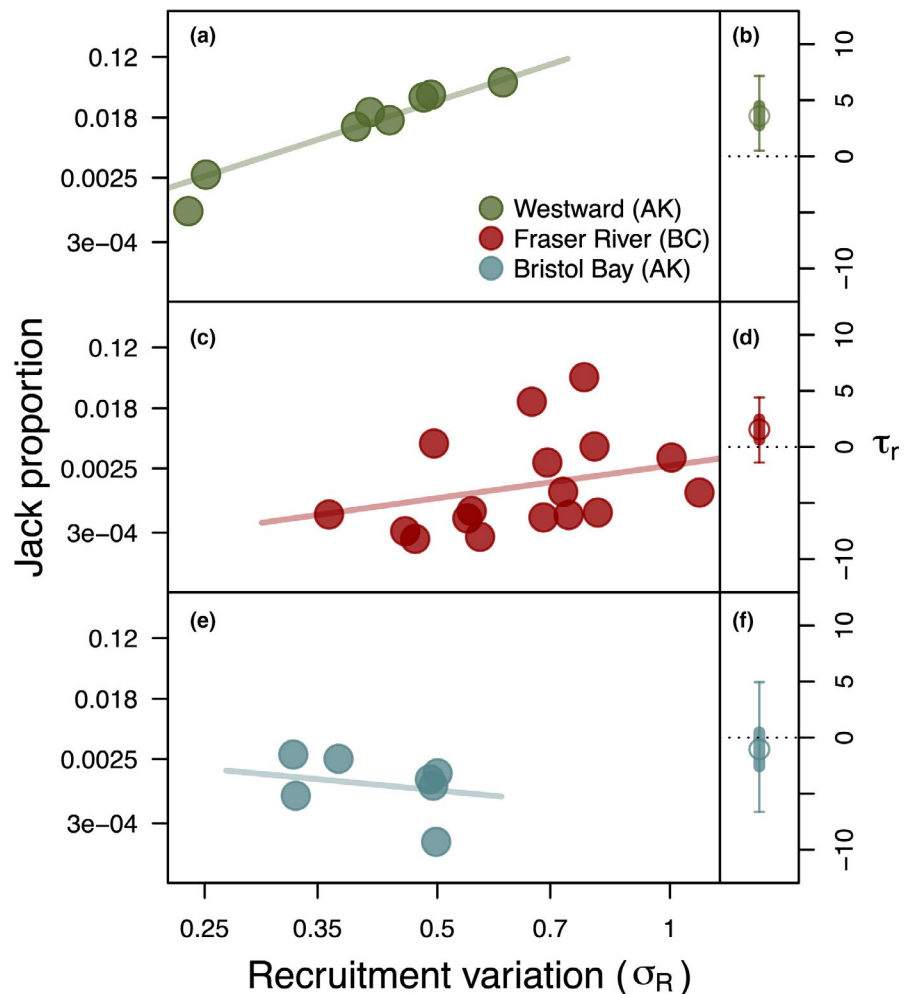
Estimated posterior distributions for coefficients (τ_r) relating a population's average jack prevalence to its recruitment variability were mostly positive for the Westward Alaska (98% positive) and Fraser River stocks (86% positive), but not for the Bristol Bay stocks (32% positive). The median value of τ_r for the Westward Alaskan stocks was 3.52 (95% credible interval = 0.14, 7.48), while that of the Fraser River was 1.54 (95% credible interval = -1.43, 4.47) and Bristol Bay exhibited an estimate of -0.93 (95% credible interval = -6.48, 4.9) (Figure 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 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 $\sigma_R = \sim 0.50$).

4 | DISCUSSION

We found that recruitment variation can substantially increase the prevalence of jacks in a population. The mechanism behind this increase appears to be the “cohort mismatch” phenomenon reported previously in a single sockeye salmon stock from Frazer Lake on

FIGURE 4 Linear relationships between the natural logarithm of recruitment variability (σ_R) and logit jack proportions by region estimated from empirical data (Table S2–S3). 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 slope of the 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. Note that the x and y-axis labels are transformed from logarithmic and logit space respectively. Figure appears in colour in the online version only



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 maturity schedule within individual year classes but will reflect the relative abundance of the different cohorts from which each maturing age class originates as well. Consequently, jacks from strong recruitment events may regularly reach maturity and spawn in the same year as older individuals from weaker recruitment events that occurred in preceding 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 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 if jacks were rare (Ayala & Campbell, 1974, Figure 1g). Given the heritability of the jack life history (Heath et al., 1994, 2002), this will then cause an elevated proportion of the ensuing cohort to be predisposed to mature as jacks as well.

By reducing the relative mean fitness of alternative life histories as they become more common, FDS is expected to shape and maintain the distribution of whatever heritable trait(s) underlie their expression (Shuster & Wade, 2003). The result should be an equilibrium distribution of trait values that reflects the fitness functions of each life-history variant (Hutchings & Myers, 1994). By extension, the population's realized tactic frequencies are expected to reflect the conditions of this equilibrium trait distribution (Gross, 1991). However, for this feedback mechanism to operate as expected, the frequencies of alternative life histories on the breeding grounds must reflect the current distribution of trait values in the population. Conversely, in Pacific salmon populations, males adopting alternative mating tactics are typically the products of different recruitment events (assuming little variation in freshwater outmigration age), such that the ratio of jacks to hooknoses on the spawning grounds each year is strongly influenced by their relative cohort sizes (DeFilippo et al., 2019). As a result, unless recruitment is constant over time, the ratio of male mating phenotypes in the breeding population is repeatedly perturbed, independent of the population's trait distribution. It has been suggested that such perturbations will make an evolutionary equilibrium difficult to achieve (Koseki & Fleming, 2006, 2007), and our results demonstrate that an additional consequence is to elevate the prevalence of the rarer male variant (i.e. jacks). Consequently, the realized frequencies of alternative male phenotypes are shaped by the magnitude of these perturbations such that jacks are more common in populations with highly variable recruitment dynamics. This effect of recruitment variation on jack prevalence represents a novel and apparently non-adaptive mechanism by which population dynamics can directly alter the life-history frequencies of age-structured populations.

The extent to which our results apply to other taxa beyond salmonids likely depends on whether alternative life histories in these species are associated with variation in age-at-maturity and heritable. For species with alternative mating tactics that are ontogenetically based (Dierkes et al., 1999; de Fraipont et al., 1993; Magnhagen, 1992; Taborsky, 1984; Taborsky et al., 1987) or largely behaviourally plastic (Barlow, 1967; Morris, 1952, 1955), it seems unlikely that recruitment variation would affect tactic frequencies. Semelparity may also be an important characteristic for generating strong cohort mismatches, as the composition of the spawning population each year will likely be less sensitive to interannual variation in recruitment for iteroparous taxa. Alternative reproductive tactics in some sunfishes (e.g. bluegill, *Lepomis macrochirus*, Centrarchidae) are associated with variation in age-at-maturity, although we know of no estimates for the heritability of these life histories (but see Dominey, 1980; Neff, 2004). It is thought that some gadids (e.g. Atlantic cod, *Gadus morhua*, Gadidae) exhibit alternative reproductive tactics as well, where spawning pairs of dominant males and females are attended by groups of satellite males which fertilize some of the eggs after release (Rowe & Hutchings, 2003). Gadids do exhibit substantial recruitment variation (Thorson et al., 2014), although it is unclear if alternative mating tactics in these species are heritable and associated with variation in age-at-maturity versus behaviourally plastic and context-dependent.

Importantly, our results show that cohort mismatches act to increase the prevalence of a given life-history variant only when it is not dominant (<50%). Therefore, it seems that rarity is also an important condition and that frequencies of alternative life histories occurring at similar levels will not be affected by stochasticity. Given that rarity and an association with age-at-maturity are required for cohort mismatches to alter life-history frequencies, our results could represent a special case of a more widespread phenomenon by which stochasticity promotes greater evenness in the distribution of maturation ages within populations. Such an effect should be even more pronounced in cases where maturation ages are not associated with alternative mating tactics subject to frequency-dependent selection, and thus may be important to maintaining variation in age-at-maturity within populations more broadly.

In addition to recruitment variation, our simulations showed that fisheries can amplify the prevalence of jacks in a population when harvest is selective for larger fish. This result is not surprising, as any increase in the mortality cost incurred by the hooknose life history is expected to lead to an evolutionary response favouring a higher equilibrium jack proportion (Gross, 1991). More broadly, previous studies have demonstrated harvest-induced shifts in population size and age structure (Hutchings, 2005; Swain et al., 2007). However, fewer 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, with virtually no response when FDS was strongest. While any increased mortality on hooknose males should increase

the relative mean fitness of jacks—and by extending their prevalence in the population—our results suggest that this may not necessarily occur as expected when FDS is an important control of male fitness. Rather, increased mortality of hooknose males does inflate the relative abundance of jacks on the spawning grounds, but the number of fertilizations actually achieved by jacks does not increase proportionally due to FDS, mediating the population's realized evolutionary response to harvest. This may explain why documented increases in the prevalence of jacks in exploited salmon populations are uncommon despite long histories of size-selective fisheries and extensive long-term monitoring data (but see DeFilippo et al., 2019; Young et al., 2020). Importantly, this result emphasizes that frequency-dependent mating (and sexual selection more broadly; Hutchings & Rowe, 2008) can filter how populations respond to fisheries-induced selection and that measurements of frequency-dependence (Berejikian et al., 2010) may be useful for predicting how alternative male life histories will respond to fishing or environmental change.

The empirical data analysed here indicated a positive relationship between a stock's level of recruitment variation and its average jack prevalence in some regions, suggesting that population dynamics can be a salient factor in the maintenance of alternative life histories in natural 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. Each Bristol Bay stock considered here is defined at the river scale and is actually composed of dozens of distinct spawning populations (Hilborn et al., 2003). Bristol Bay sockeye salmon are known for their biocomplexity and the stabilizing effect that this population diversity exerts on their aggregate dynamics (Schindler et al., 2010). As such, recruitment variation measured at the river scale is not representative of the realized variability within individual spawning units. While the other stocks considered here are also composites of multiple subpopulations, their biocomplexity is not as extensive as that of Bristol Bay (Griffiths et al., 2014). More importantly, enumeration of jacks may be more difficult for Bristol Bay stocks. For instance, abundance and age composition are estimated using weirs at 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 lower jack proportions and lack of contrast among Bristol Bay stocks (Figure 4e). Finally, there may simply be other mechanisms not accounted for in our analysis, such as exploitation history (e.g. harvest rate/size selectivity), the strength of frequency-dependence, or spawning habitat conditions (DeFilippo et al., 2018) which are important in shaping the dynamics of alternative life histories in Bristol Bay sockeye salmon.

Uncertainty in parameter values and functional forms assumed (e.g. alternative forms of frequency-dependent selection), and the influences of additional factors not considered here (e.g. fine-scale habitat heterogeneity, behavioural plasticity) may affect the

dynamics of alternative life histories beyond what our simulations account for. Moreover, the genetic basis 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, 2021) and previous studies have shown that the genetic architecture of a trait can have important effects on how it responds to selection (Kuparinen & Hutchings, 2017; Oomen et al. 2020). In particular, there is growing evidence for a genetic architecture of age-at-maturity in salmon that includes regions of large effect (McKinney et al., 2019, 2021), which likely has important implications for life-history evolution and maintenance. While the empirical results presented here, and those of previous studies (DeFilippo et al., 2019) suggest that the phenomena presented in our simulations do occur in real-world populations, any specific predictions for individual populations should be based on studies parameterized to reflect their specific conditions. While theoretical models have often considered the effects of stochasticity on life-history evolution through indirect pathways such as environmental heterogeneity or variability (Lively, 1986; Murphy, 1968; Roff, 1975; Winemiller & Rose, 1992), few studies have considered the effects of stochasticity being propagated through population dynamics. Our results provide a heuristic demonstration of how such interactions can reshape the maintenance of alternative life histories that we hope will stimulate further investigations.

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 behaviour of natural populations (Stockwell et al., 2003). Here, we demonstrate that recruitment variation can interact with selection to produce emergent dynamics that could not be predicted from a purely evolutionary viewpoint. ARTs are particularly common in fishes (Taborsky, 2008), and many fish populations are also characterized by persistent stochastic variability (Thorson et al., 2014). Consequently, models of ARTs in fishes should consider the effects of non-equilibrium population dynamics (Vincent & Brown, 1987). To the extent that ARTs can affect the management of commercially valuable fish stocks, predicting their responses to environmental change or harvest 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 (Worden et al., 2010). Closed-loop simulations (Punt et al., 2016) that account for some of the mechanisms identified here may be particularly useful for evaluating how different harvest, management or environmental scenarios could affect the maintenance of alternative life histories.

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DATA AVAILABILITY STATEMENT

All data used in this analysis are publicly available upon request from the Alaska Department of Fish and Game (ADF&G) and The Pacific Salmon Commission/Department of Fisheries and Oceans (DFO), Canada. The simulation model code and output from this study are available from: https://github.com/lukasdefilippo/Life_Hist_IBM

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SUPPORTING INFORMATION

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