

Modeling local adaptation and gene flow in sockeye salmon

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Abstract. Microevolutionary processes determine levels of local adaptation within populations and presumably affect population productivity, but selection and phenotypic evolution have not often been linked explicitly to population dynamics in the wild. Here, we describe a stochastic, individual-based model that simulates evolutionary and demographic effects of migration and selection in interconnected sockeye salmon populations. Two populations were simulated based on parameters obtained empirically from wild populations in the Bristol Bay region of southwestern Alaska, representing beach- and stream-spawning ecotypes. Individuals underwent a full salmonid life cycle, experiencing sexual selection, size-selective harvest, and predation based on body size at maturity. Stabilizing natural selection on the three traits (body length, body depth, and age at maturity) tracked for all individuals favored different phenotypes in the two ecotype populations, and the three traits evolved in a genetically correlated manner. Simulation results showed that stabilizing selection on fish phenotypes was always critical for maintaining local adaptation, especially when dispersal rates were high, but loss of local adaptation did not result in substantial loss of productivity. Rather, productivity was more strongly influenced by the opposing effects of stabilizing and harvest selection; strong stabilizing selection caused the salmon to evolve larger body sizes that made them more likely to be caught in the fishery. The model results suggest that interactions between different selection pressures can have substantial demographic as well as evolutionary consequences in wild salmon populations, with key implications for sustainability of natural production in the face of selective harvest and systemic environmental change.

Key words: gene flow; human-induced evolution; individual-based model; local adaptation; natural selection; population dynamics.

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INTRODUCTION

Local adaptation is the process by which natural selection increases the frequency of traits that confer a fitness advantage under local environmental conditions. In theory, local adaptation within a metapopulation is driven by diversifying selection, opposed by gene flow and temporal variation in selection, confounded by genetic drift, and constrained by genetic variation (Kawecki

and Ebert 2004, Peterson et al. 2014). Increased genetic variation increases the efficacy of selection, which can promote local adaptation. In contrast, genetic drift reduces evolutionary potential by causing random loss of genetic variation, especially in small populations (Stockwell et al. 2003). For larger populations, the interaction between selection and gene flow is the primary determinant of local adaptation. Gene flow generally reduces differentiation between populations but

can either impede or encourage adaptive divergence, depending on its level and the characteristics of the dispersers (Garant et al. 2007). Selection will tend to increase local adaptation, although different selection pressures may have opposing effects on mean trait values within a population. Although the theoretical effects of these microevolutionary forces are well understood, their relative importance in determining local adaptation in most wild populations is not.

Local adaptation is relevant to population management because it relates to fitness and population productivity (Taylor 1991), but linking trait evolution and local adaptation directly to wild population dynamics is difficult to accomplish empirically (see Coulson et al. 2006, 2010, and Pelletier et al. 2007 for notable exceptions). A growing body of literature indicates that local adaptation can develop over just tens of generations (Kinnison et al. 2007), but identifying the relative impacts of different microevolutionary forces on local adaptation is challenging because the forces interact in complex ways. Studying phenotypic trends in long-term data sets without comparable control populations is insufficient, as such data are determined by both genetic and environmental variation, which can preclude the demonstration of evolutionary change (Hard et al. 2008). However, laboratory experiments and modeling studies may provide valuable insights and produce hypotheses that are testable in wild populations.

One method for identifying microevolutionary change is captive breeding experiments, which allow for direct manipulation of populations and observation of phenotypic responses to evolution (Conover and Munch 2002). Unfortunately, the number of species that can realistically be used for such experiments are limited, and laboratory-induced artifacts may affect results (Harshman and Hoffmann 2000). It is also possible to study wild populations intensively by pedigree analysis, which can provide data on both quantitative genetic parameters and selection gradients (Garant and Kruuk 2005, Pemberton 2008). However, pedigree studies are only feasible for populations where all or most breeding adults can be sampled, which means they are more generally applied to small populations that are subject to high genetic drift and may be atypical. Natural populations also experience temporal variation

in selection (Siepielski et al. 2009), which complicates predictions of evolutionary change.

Simulation modeling is a flexible approach for considering how evolution may affect population diversity and productivity. Quantitative genetic models in particular are useful for determining potential evolutionary responses to selection, and they can be coupled with age- or stage-structured models to simulate consequent effects on population dynamics (Law 1991, Hard 2004, Eldridge et al. 2010). Integral projection models (IPMs) also predict evolutionary change but are based on temporal integration of continuous traits across the life cycle rather than stage-based matrix analysis. Integral projection models require estimation of fewer parameters (Ellner and Rees 2006) but rely on functions describing the associations between observed traits and survival, fertility, trait development, and offspring trait values (Coulson et al. 2010). Both deterministic age- or stage-structured models and IPMs are useful for simulating evolutionary and demographic trends over time, but they do not explicitly consider variability among individuals, which can alter evolutionary outcomes (Wilson 1998, Coulson et al. 2004). Inference from IPMs can also be substantially influenced by the limitations of the development and inheritance functions that are used to construct them (Janeiro et al. 2016). Individual-based models (IBMs) are another type of simulation that is useful for considering variation among individuals resulting from stochastic events (Grimm 1999), and they can readily incorporate age or stage structure. Although computationally intensive, they provide a flexible approach to simulating evolutionary responses and can also be used to study population dynamics, especially where individual variability may have substantial demographic effects (Huston et al. 1988). For example, Ronce and Kirkpatrick (2001) developed an individual-based, quantitative genetic model to assess how dispersal might affect evolution and population dynamics of two populations using different habitat types. They found a dispersal threshold above which increasing connectivity caused maladaptation and a dramatic population size decrease in one of the habitats, a phenomenon they termed “migrational meltdown.” However, their model focused on differences between specialist and generalist species and did not include many stochastic components.

In another example, a stochastic quantitative genetic IBM was used to investigate how fisheries selection might have reduced age and size at maturity in Chinook salmon (*Oncorhynchus tshawytscha*) populations spawning in western Alaska (Bromaghin et al. 2011). This model simulated a single population of salmon, and population dynamics were affected by survival at different stages within the Chinook salmon life cycle. Specifically, fish experienced density-dependent survival in early life stages, followed by stabilizing selection on body size, size-selective harvest, assortative mating, and size-dependent determination of fecundity. Individual body length and age at maturity were tracked, and empirically estimated heritabilities for these traits were used to simulate genetic variation in fish phenotypes. The model suggested that harvest often resulted in directional selection for lower mean age and size at maturity, and that reducing exploitation rates and gillnet mesh sizes simultaneously was relatively effective at stimulating phenotypic recovery of size and age.

Here, we extended the model developed by Bromaghin et al. (2011) to determine how connectivity between salmon populations might affect their evolution and demography. First, we added the ability to model correlated evolution among multiple traits using genetic variance–covariance (G) matrices (Lande 1979). Multivariate models are capable of more fully characterizing the effects of selection on phenotypes in a population, as phenotypic traits are often genetically linked and do not evolve independently (Lande and Arnold 1983, Law 1991, Hard 2004). Second, we modeled two wild sockeye salmon (*Oncorhynchus nerka*) populations from distinct habitats and allowed for dispersal between the populations to assess the effects of gene flow on local adaptation and population productivity (measured as in-river return rate). To our knowledge, no previously published IBMs of salmon have included multiple populations connected by gene flow, even though most wild spawning populations are not isolated and do exchange breeders with nearby populations (Policansky and Magnuson 1998). Indeed, metapopulation dynamics are thought to affect salmonid population persistence on both ecological and evolutionary time scales (Schtickzelle and Quinn 2007).

Population connectivity may be particularly relevant in situations where phenotypically distinct populations have the opportunity to interbreed. For example, stream- and beach-spawning ecotypes of sockeye salmon utilize different spawning habitat and sometimes show striking morphological differences (Quinn 2005). Beach spawners encounter less bear predation, leading to sexual selection for greater body depth (Blair et al. 1993), whereas stream spawners are often exposed to higher predation and stranding risk that may result in selection for smaller body sizes (Quinn et al. 2001a, Lin et al. 2016). To study how connectivity and selection might affect the potential for phenotypic divergence between ecotypes, we parameterized the model using empirical data collected from sockeye salmon beach- and stream-spawning populations in Little Togiak Lake (Wood River Lakes system, southwestern Alaska). Beach and stream spawner populations often occur in close geographic proximity, and previous work suggests that they can be differentiated genetically despite the apparent lack of physical barriers to dispersal (Lin et al. 2008). Thus, interactions between adaptive divergence and gene flow potentially impact evolution and maintenance of these ecotypes.

Our overall aim was to develop and use this model to predict how opposing selection pressures and varying dispersal rates would affect local adaptation and population sizes in beach and stream ecotypes of sockeye salmon. Our first objective was to determine the effects of the different selection submodels on phenotypic trait distributions and population sizes. Although each selection submodel was based on best available information and parameterized using empirical data on sockeye salmon, interactions among the different submodels were potentially complex, and we were interested in examining the effects of these interactions. Our second objective was to examine the effects of the balance between gene flow and stabilizing selection within populations on demography, with the a priori expectation that high gene flow would reduce local adaptation and, consequently, population productivity. In running these model experiments, we hoped to demonstrate the potential utility of this model in linking evolution and population dynamics.

METHODS

Overview

Conceptually, the model linked evolution and population dynamics as follows. We simulated two sockeye salmon populations linked by gene flow, one representing the stream ecotype and one representing the beach ecotype. Individuals proceed through a full anadromous salmonid life cycle (Fig. 1), and the model tracks individual body length, body depth, and age at maturity. After the populations are initialized and have experienced age-specific natural mortality in freshwater and in the ocean, the fish are subjected to harvest as they return to freshwater as adults to spawn. Most of the surviving fish return to the population of origin, but some individuals disperse to the other population. Fish returning to the stream population encounter size-selective bear predation. Surviving fish then mate, with each female spawning and choosing a single male mate based on his body length (larger males have higher mating success). Female fecundity determines the number of offspring produced per mating, and total offspring numbers are initially reduced using a density-dependent parameterization of the Ricker stock–recruit model, which is commonly used for exploited anadromous species (Ricker 1954). The traits of the survivors are then determined by a multivariate quantitative genetic model, which combines parental breeding values and environmental stochasticity to produce individual phenotypes. After undergoing

annual, density-independent marine survival rates, individuals are subjected to stabilizing selection based on their trait values at maturity, such that individuals with trait values deviating from the local population optimum are less likely to survive to maturity. Recruits (immature fish that are susceptible to harvest) undergo harvest selection as they return to spawn, completing the life cycle.

In the model, we applied stabilizing selection on body size traits at maturity assuming that the trait values observed in nature reflect natural or sexual selection on size and age in each population. This model was conceptualized as selection that would tend to disfavor individuals whose phenotypes deviated greatly from the target mean size and age—that is, a force that might reflect natural or sexual selection on size and age in the population. We used this approach to parameterize fitness in our model. We did not specifically model the ecological processes that might lead to this type of selection, because we did not have the necessary information to support it. Hence, we considered stabilizing selection to be a multifaceted factor for which we have little information, which was a limitation of our model. However, stabilizing selection is a critical evolutionary factor operating in natural populations and is thought to be important to include to reflect the process of local adaptation (Hard 2004).

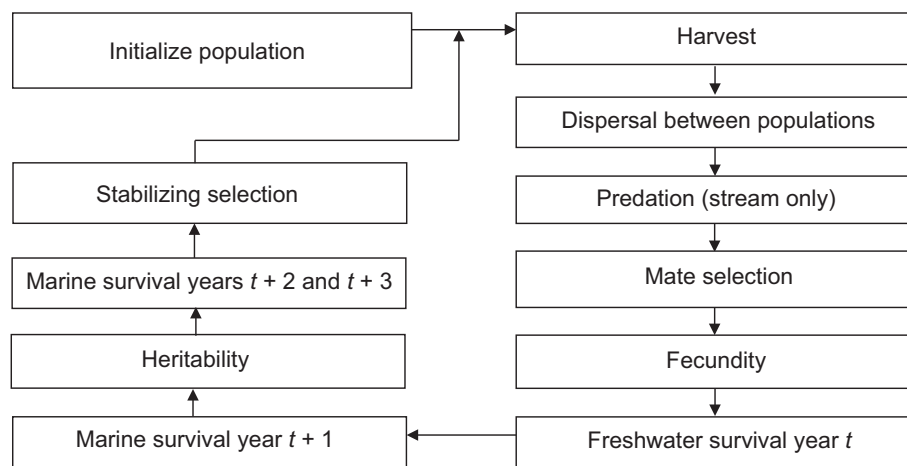


Fig. 1. Flowchart of simulation model processes.

When modeling trait evolution, we assumed additive breeding values and an infinitesimal genetic model, such that trait values were determined by many unknown genes of small phenotypic effect. The model did not consider effects of mutation or evolution of genetic variance. We also assumed a joint multivariate normal distribution for both breeding values and phenotypes (Lande and Arnold 1983). The model description below includes aspects of a recommended protocol for describing IBMs (Grimm et al. 2006). The simulation code was primarily written in R version 2.11.1 and updated to R version 3.4.2 (RDCT 2017); the mating submodel was coded in Fortran 95 (Metcalf et al. 2004) and compiled using the free-ware G95 compiler (<http://www.g95.org>).

State variables and scales

The model has two hierarchical levels: individuals and populations. For each population, individual adult salmon are characterized in terms of sex, population of origin, and three traits that can affect reproductive fitness: adult body length (mm), adult body depth (mm), and age at maturity (yr). Age is tracked as a discrete variable, with individual maturing at 3, 4, or 5 yr of age. Unless otherwise stated (see *Harvest submodel*), body length is defined as the linear measurement from the mid-eye to the hypural plate, and body depth is defined as the linear distance from the anterior insertion of the dorsal fin to the belly, perpendicular to the long axis of the fish. We use these morphological measures because they are also used in the field in the Wood River Lakes system (Blair et al. 1993). The model runs on a yearly time step with discrete events within the year, as we are primarily interested in how adult trait distributions and adult numbers in the two populations change over time.

Process outline and scheduling

Each simulation had individuals proceed through a sequence of stages occurring within the life history of sockeye salmon (Fig. 1). Demographic processes consisted of stage-specific survival and reproduction, and evolutionary processes determined individual phenotypic traits based on the traits of the parents. Two models were run in sequence. The first was a burn-in model that initialized the populations and allowed them to evolve in reproductive isolation.

This burn-in was run for a sufficient length of time to ensure that the population dynamics and phenotypes were temporally stable, generally for 1000 yr. Annual returns simulated during the burn-in were then randomly grouped into blocks of five years each. Each five-year block was used to initiate a simulation replicate in the primary simulation model, which was structured similarly to the burn-in model but included dispersal between populations.

Input

Empirical estimates of parameter values were derived from two wild populations of beach- and stream-type sockeye salmon, the A Creek and A Beach populations, located in Little Togiak Lake in the Wood River Lakes system in southwestern Alaska (Lin et al. 2008). Overall means and standard deviations for body length and depth at maturity (Table 1) were estimated from thousands of A Creek adults (2368 females and 1405 males) and from hundreds of A Beach adults (235 females and 146 males). Means and standard deviations for age at maturity (Table 1) were estimated from 748 females and 321 males in the A Creek population and from 30 females and 12 males in the A Beach population. Morphological data from these aged individuals were also used to estimate phenotypic variance-covariance

Table 1. Means and standard deviations of trait values at maturity for beach- and stream-spawning sockeye salmon, calculated from empirical data collected on A Creek and A Beach in Little Togiak Lake, Alaska.

Trait	Stream female	Stream male	Beach female	Beach male
Mean age (yr)	4.2	4.3	4.3	4.1
	4.5	4.5	5.2	5.2
SD age (yr)	0.4	0.5	0.5	0.3
	0.4	0.6	0.6	0.6
Mean length (mm)	422	430	436	470
	430	440	460	490
SD length (mm)	28	34	32	39
	30	35	35	35
Mean depth (mm)	105	125	113	167
	115	140	135	180
SD depth (mm)	10	15	15	27
	15	20	15	20
Cut-point, ages 3–4	2	2	2	2
Cut-point, ages 4–5	4.5	4.5	4.2	4.2

Notes: Above: values before model calibration. Below: values after model calibration (for all data except age cut-points).

Table 2. Phenotypic variance–covariance matrices for each sex and population, calculated from empirical data on A Creek and A Beach sockeye salmon.

Population	Female	Male
Stream	$\begin{bmatrix} 0.2 & 5.7 & 1.4 \\ 5.7 & 763.8 & 171.6 \\ 1.4 & 171.6 & 112.5 \end{bmatrix}$	$\begin{bmatrix} 0.2 & 9.1 & 3.1 \\ 9.1 & 1136.6 & 346.0 \\ 3.1 & 346.0 & 222.5 \end{bmatrix}$
Beach	$\begin{bmatrix} 0.2 & 9.3 & 5.9 \\ 9.3 & 726.2 & 282.7 \\ 5.9 & 282.7 & 281.4 \end{bmatrix}$	$\begin{bmatrix} 0.2 & 4.8 & 3.0 \\ 4.8 & 997.4 & 369.8 \\ 3.0 & 369.8 & 280.6 \end{bmatrix}$

Note: In each of these matrices, the first trait is age at maturity (yr), the second trait is body length at maturity (mm), and the third trait is body depth at maturity (mm).

matrices for age, body length, and body depth at maturity (Table 2). Trait variances within each population and sex composed the diagonal elements of each matrix, and pairwise covariances between traits composed the off-diagonal elements. All of these phenotypic parameter values were used as inputs for initiating trait values in the simulated populations but did undergo some adjustments (see *Model calibration*).

Quantitative genetic parameters (heritabilities for body length and body depth at maturity, genetic correlation between body length and body depth) were estimated from pedigree data from the A Creek population using an animal model (see Lin et al. 2016 for details). To reconstruct the pedigree for the 2004 brood year, all spawning adults were sampled from 2004 to 2009, as over 99% of individuals mature at total ages of 4 to 5 yr. These A Creek individuals were genotyped at 11 DNA microsatellite markers, and a pedigree was reconstructed via maximum-likelihood methods with the software program COLONY V. 2 (Jones and Wang 2010). The COLONY parentage assignments were confirmed using a data set of 80 single nucleotide polymorphisms (Hauser et al. 2011). Quantitative genetic parameters were estimated from the constructed pedigree using the MCMCglmm package in R (Hadfield 2010). The estimated genetic covariance between body length and depth was 0.79, and narrow-sense heritability (h^2) estimates were 0.58 and 0.31 for length and depth, respectively (Lin et al. 2016). Heritability was not estimated for age at maturity because we did not have age data for most of the pedigreed individuals.

In a quantitative genetic framework, trait evolution depends heavily on the genetic variance–

covariance matrix G , a square matrix that describes the additive genetic variances of phenotypic traits and the genetic covariances among traits. For our model, $G = h^2 \times P$, where P is a phenotypic variance–covariance matrix. We calculated P based on empirical estimates of trait variances and covariances at age, resulting in a 3-by-3 matrix for each population that included body length, body depth, and age at maturity. We assumed an h^2 value of 0.3, which was the smaller of the two heritability values estimated empirically and consistent with other estimates of heritability for these traits in salmonids (Carlson and Seamons 2008). Lower values of heritability could constrain the effects of migration on trait phenotypes, but we decided to use them because sensitivity analyses of the results to variation in heritability (results not shown) had only nominal effects. We note that from the animal model analyses, the low values of heritability primarily reflect higher values of residual environmental variance rather than lower values of additive genetic variance.

One important consideration for the model was whether genetic covariances between traits were positive or negative, because the sign of the covariance fundamentally determines potential evolutionary responses. The genetic covariance estimated directly from A Creek pedigree data (0.79), and the covariances in the estimated G matrices all indicated a positive genetic covariance between body length and body depth (Lin et al. 2016).

A potential complication for predicting evolution is that the G matrix is expected to evolve over time in response to microevolution (Steppan et al. 2002, Jones et al. 2003). Assumptions of normality and a constant G are unlikely to be seriously violated when either the effective number of migrants (N_{em}) or phenotypic differences between populations are small, but higher rates of gene flow may affect the shape and orientation of G (Guillaume and Whitlock 2007). However, we are not aware of any current analytical methods for predicting the evolution of G in finite populations (Arnold et al. 2008), and we therefore have not modeled evolutionary change in G .

Population initialization

The phenotypic data described above were used to create the initial salmon populations

used in the model. Individuals and their trait values at maturity were randomly generated from a multivariate normal distribution based on the estimated trait means and standard deviations (see Table 1) as well as the estimated phenotypic covariance matrices. As a result, age at maturity was generated as a continuous variable, henceforth referred to as continuous age. However, a discrete age at maturity was also required to determine when fish returned to freshwater as adults. Age cut-points were therefore created to separate fish into discrete age categories based on their continuous ages; for instance, if the age 3-to-4 cut-point was set at 3.5, an individual with a continuous age of 3.1 would be categorized as age 3. These cut-points (see Table 1) were initially set at 3.5 (ages 3–4) and 4.5 (ages 4–5) but were adjusted during model calibration (see *Model calibration*).

Model calibration

Because some submodels had opposing selective effects on fish body size, the model required some adjustment to produce realistic fish phenotypes. We calibrated the model by monitoring a subset of outputs that were deemed most important, changing specific phenotypic parameters (age cut-points and means and standard deviations of body length, body depth, and age at maturity) to produce temporally stable patterns in the chosen outputs (following Beaudouin et al. 2008, Bromaghin et al. 2011). These parameters reflected stabilizing selection on the traits. The selected outputs were the means and variances of (1) proportion of age-4 spawners, (2) body length at maturity, (3) body depth at maturity, and (4) the number of spawners per year. When these outputs deviated markedly from values expected from empirical observations, the model was re-run after slightly changing initialization parameters, namely the age cut-points and means and standard deviations of body length, body depth, and age at maturity. Final parameter values used for population initialization are presented in Table 1.

Submodels

Submodels are ordered chronologically along the salmon life cycle, starting with individuals that undergo harvest. This is also the order of computational processes in the model (Fig. 1).

Harvest submodel.—Sockeye salmon are subject to substantial harvest exploitation during their spawning migration, which can remove as many as 75% of individuals per year in some fishing districts (Kendall et al. 2009). Size-specific estimates of fishery selection on sockeye salmon have been obtained for both the Nushagak district as a whole (Kendall et al. 2009) and for some individual populations in the Wood River Lakes system (Kendall and Quinn 2009). These studies suggest that the type and intensity of selection have varied over time and between sexes, but across all Nushagak district populations, the fishery catches more males than females and exploits populations with larger, older fish more heavily (Kendall et al. 2009). Size selectivity is greater in populations with relatively small fish, because the difference in harvest vulnerability between larger and smaller fish within these populations is more pronounced than it is in populations with larger fish overall (Kendall and Quinn 2009).

Forty-seven years of fisheries data (1963–2009) for the Wood River Lakes system have been assembled and analyzed (Cunningham et al. 2013). Catch data were separated by sex and grouped into 10 mm body length bins, and the proportion captured was calculated for each bin. Gaussian distributions were fit to the data, assuming a binomial error distribution because data were proportions. The parameters α , μ , and σ determine the shape of the distributions, where α is a scaling factor that determines the maximum possible selectivity, μ is the body length of maximum selectivity (mean of the distribution), and σ determines the relative selectivities of lengths above and below the peak (standard deviation of the distribution). The capture probability for each individual in the model was calculated as:

$$P_{\text{capture}} = \alpha \times \exp\left(-\frac{(\text{fork length} - \mu)^2}{2 \times \sigma^2}\right)$$

Parameter values were as follows: $\alpha = 0.55$, $\mu = 533.0$, $\sigma = 122.2$ for females, and $\alpha = 0.65$, $\mu = 539.7$, $\sigma = 107.1$ for males. Body lengths within the harvest submodel were defined as measurements from the mid-eye of the fish to the fork of the tail (fork lengths in mm), because these are the length data taken in the fishery.

Equations provided in Kendall and Quinn (2009) were used to convert between this fork length and the mid-eye–hypural plate lengths used in the rest of the model. Based on these harvest selectivity curves and the distributions of optimum body lengths in each population, selectivity was expected to be higher on the stream population than the beach population, in that harvest would lead to stronger directional selection for smaller body size in the stream population.

Dispersal submodel.—Dispersal rates, defined as the proportion of a population that strayed to the other population, were set by the user and were random with respect to fish phenotype. A cut-point value was selected to capture the specified proportion of a random normal distribution (mean = 0, standard deviation = 1), and each individual within a population was assigned a random number drawn from that same distribution. Individuals with assigned values below the cut-point were designated as dispersers.

Predation submodel.—Bears are important agents of natural selection on sockeye salmon in streams (Quinn and Kinnison 1999, Lin et al. 2016), removing approximately 12–96% of adults within each spawning population each year (Quinn et al. 2003). Prior research also suggests increased predation risk for fish with larger than average body sizes (Quinn and Buck 2001, Carlson and Quinn 2007) and for males as compared to females (Ruggerone et al. 2000). We therefore applied sex-specific predation selection models with increased predation risk for larger individuals homing or straying to the stream population. Fourteen years of detailed data on individual modes of death (bear-killed versus senescent) were obtained from Hansen Creek, a well-studied stream in the Wood River Lakes system (C. Cunningham, unpublished data). These data were separated by sex and grouped into 10 mm body length bins, and the proportion of bear-killed fish was calculated for each bin.

In the model, bear-killed individuals die before reproducing, but in reality predation does not completely eliminate fitness of killed spawners because individuals may reproduce successfully before being preyed upon. Comparisons of reproductive lifespans (days between stream entry and death) between bear-killed and senescent fish in C Creek, a Wood River Lakes system stream similar in size to A Creek, indicated that

the in-stream lifespan of bear-killed females was about 65% that of senescent females and that bear-killed males lived about half (50%) as long as senescent males. Assuming that reproductive lifespan relates to fitness, we multiplied the probability of predation derived from Hansen Creek data by the expected reduction in reproductive lifespan (0.35 for females, 0.50 for males), producing an adjusted probability of predation. Linear selection models were fitted to the adjusted probability of predation, using mid-eye–hypural plate body length (L) minus the body length of an individual with an expected predation probability of zero (L_{POF} for females, L_{POM} for males) as the independent variable. The following sex-specific predation models were the result.

$$P_{\text{predation, females}} = 0.0013 \times (L - L_{POF})$$

$$P_{\text{predation, males}} = 0.0014 \times (L - L_{POM})$$

The predation submodel was not applied to the simulated beach-spawning populations, as the risk of bear predation on sockeye salmon in beach habitat is generally considered much lower than in streams (Quinn et al. 2001b). Nevertheless, it was included in the baseline model simulation to evaluate the potential selective effects of removal of some larger beach spawners by bears, and so that results would be more directly comparable between beach and stream baseline scenarios.

Mating submodel.—The mating submodel paired males and females in two stages, following Bromaghin et al. (2011). Each male had a probability of proposing to a female, and in turn, the female had a probability of accepting a proposal. Probability of proposal or acceptance was described by a quadratic logistic function with a restricted range:

$$P_{\text{proposal/acceptance}} = a + (b - a) \left[1 + e^{-\beta_0 - \beta_1 x - \beta_2 x^2} \right]^{-1}$$

where x is the ratio of female to male body length, and $a = 0.05$, $b = 0.95$, $\beta_0 = -10$, $\beta_1 = 10$, and $\beta_2 = 3$ (Bromaghin et al. 2011). For a given female, a male was randomly selected from all males that returned to spawn (i.e., in the escapement), and the probability of success for that particular mating was determined using the product of the proposal and acceptance probabilities. If mating was unsuccessful, additional males were chosen until mating occurred. The process proceeded sequentially until all females mated exactly once. Mating was

somewhat assortative with respect to body length because the probability of mating success increased as x approached the value of one; the overall correlation between mate lengths was about 0.2.

Fecundity submodel.—Fecundity and body length data collected on sockeye salmon spawning in Hansen Creek in the Wood River Lakes system ($n = 106$; J. Lin, unpublished data; see also Quinn et al. 2006) were used to infer the relationship between fecundity and female body length. Plotting body length in mm (L) minus the body length of a fish with an expected fecundity of zero (L_{F0}) against total fecundity indicated a linear relationship of the form:

$$\text{fecundity} = 11.54 \times (L - L_{F0})$$

An additional constant was drawn from a random normal distribution (mean = 0, variance = 100) and added to the calculated fecundities to make them stochastic. To prevent unreasonably small fecundity values (Bromaghin et al. 2011), the minimum fecundity was set at 2000 eggs, a value close to the lowest observed fecundity observed in the Hansen Creek data set (2383 eggs).

Survival submodel.—Survival rates were applied to all individuals each year until they became recruits, including the first year of growth in freshwater and each year spent in the ocean. For example, an individual that matured at four years of age had to survive one year in freshwater and three years in the ocean, experiencing a total of four mortality culls.

Total survival to recruitment was based on a reparameterization of the Ricker productivity model (Ricker 1975). Following the framework developed by Bromaghin et al. (2011), annual freshwater and marine survival rates were calculated so that the number of recruits (R) surviving from the total number of eggs deposited by the escapement (E) reflected the number of recruits expected from a parent stock of size S_r , the replacement abundance when the number of recruits is equivalent to the size of the parent stock (i.e., the steady-state stock size).

$$R = E \left(\frac{-\alpha E}{e^{\mu_F S_r}} \right) \left(\frac{e^\alpha}{\mu_F} \right)$$

The parameter α controls the shape of the stock–recruitment relationship (recruits per spawner at low spawner abundance), and μ_F is the mean number of eggs per spawner. The parameter α

was set at 2.25, a value derived from Yukon River Chinook salmon run reconstructions (described in Bromaghin et al. 2011). Empirical fecundity data were used to estimate μ_F : The mean number of eggs per female was 3000, and assuming an equal sex ratio, 3000 was multiplied by 0.5 to obtain 1500 mean eggs per spawner.

In the above equation, the first component in parentheses is a density-dependent survival rate, and the second component is a density-independent survival rate. Average freshwater survival rate λ_F from egg stage to through the first year in freshwater was considered equivalent to the density-dependent rate:

$$\lambda_F = \exp \left(\frac{-\alpha E}{\mu_F S_r} \right)$$

The density-independent rate was then approximately equivalent to the product of all annual marine survival rates:

$$\left(\frac{e^\alpha}{\mu_F} \right) = \lambda_{M1} \left(\frac{\lambda_{MF} + \lambda_{MM}}{2} \right)^{\left(\frac{\mu_{AF} + \mu_{AM}}{2} - 3 \right)}$$

where λ_{M1} is mean survival in the first year in the marine environment, μ_{AF} and μ_{AM} are the mean ages at maturation for females and males, respectively, and λ_{MF} and λ_{MM} are the sex-specific annual marine survival rates from age 3 to maturity for females and males, respectively. The survival rates λ_{MF} and λ_{MM} were drawn randomly each year from a lognormal distribution with mean $\ln(0.8)$ and standard deviation 1.05, and the survival rates were assumed constant for the second to fourth years of marine residency within each cohort generated that year. These mean and standard deviation values were chosen to generate marine survival rates comparable to those published in the literature (Rensel et al. 2010). λ_{M1} was assumed equal for both sexes and calculated as:

$$\lambda_{M1} = \left(\frac{e^\alpha}{\mu_F} \right) \div \left[\left(\frac{\lambda_{MF} + \lambda_{MM}}{2} \right)^{\left(\frac{\mu_{AF} + \mu_{AM}}{2} - 3 \right)} \right]$$

The mean lifetime fitness λ for an individual of sex G maturing at age A was then:

$$\lambda = \lambda_F \lambda_{M1} (\lambda_{MG})^{A-3}$$

Heritability submodel.—The heritability submodel generated offspring phenotypes based on

the concept that the variability of a phenotype (X) is the sum of its genetic (G) and environmental (E) components of variation (Roff 2010):

$$X = G + E$$

Evolution was measured in terms of changes in mean breeding values of traits over time, with an individual's breeding value defined as the mean expected trait value of its adult progeny, equivalent to the genetic component of an offspring's phenotype. Specifically, under the assumption of an infinitesimal model, an individual's breeding values were calculated as its midparent breeding values (z_1 and z_2) plus a genetic deviation ε drawn from a multivariate normal distribution with a zero mean vector and covariance matrix equal to 0.5 times the G matrix (Tufto 2010):

$$z = \frac{1}{2}(z_1 + z_2) + \varepsilon$$

Selection acts directly upon traits as they are expressed in phenotypes. Phenotypes were calculated as breeding values plus an environmental deviation, which was drawn from a multivariate normal distribution with a zero mean vector and a covariance matrix of residual deviations R , where $R = P - G$.

Additionally, sex-specific trait values were calculated for each family group due to the sexual dimorphism in age and size at maturity observed in sockeye salmon. To perform the sex-specific calculations, trait data for each individual were transformed from one sex to the other using Cholesky factorizations of the sex-specific trait distributions (Bromaghin et al. 2011). This process tended to produce some phenotypes more extreme than those observed empirically; therefore, after the phenotypes of each offspring were determined, we applied sex-specific lower and upper bounds on body length and depth for each age class at maturity to prevent unrealistic phenotypes from being generated. For age-3 fish, upper and lower bounds were set to 90% and 110% of the observed trait means (data available only for A Creek males). For age-4 and age-5 individuals, the bounds were set to 85% and 115% of observed trait means, averaged between the beach and stream populations.

Fitness submodel under stabilizing selection.—The fitness submodel applied stabilizing selection to newly produced recruits each year, based on

their predicted trait values at maturity. This submodel selects against individuals with phenotypes that deviate from the population optimum, which was determined by initial mean trait values. Each individual was assigned a fitness weight, calculated using the following equation (adapted from Lande 1979):

$$W(z) = \exp \left[-\frac{1}{2 \times y} (z - \theta)^T \omega^{-1} (z - \theta) \right]$$

where y is a scaling factor that scales fitness weights to a minimum of 0 and a maximum of 1, z is a vector of trait values for an individual (body length, body depth, and age at maturity), θ is a column vector of trait optima, and ω is a matrix describing the curvature and orientation of the fitness landscape (sensu Simpson 1944) for the multiple traits represented in the population.

Conceptually, ω describes the curvature and orientation of a Gaussian fitness peak on the fitness landscape. The diagonal elements of ω correspond to the strength of stabilizing selection for each trait, and the off-diagonals correspond to the strength of correlational selection between traits. When the diagonal elements are large, ω describes a wider adaptive peak with less curvature and hence weaker stabilizing selection (Arnold et al. 2001). All of the elements together determine the correlation of selection r_s , which is calculated as $r_s = \omega_{12} / \sqrt{\omega_{11}\omega_{22}}$ in the bivariate case (Guillaume and Whitlock 2007). When r_s is larger, the major axis of the adaptive peak is less parallel to the character axes, which increases the efficacy of simultaneous stabilizing selection on all traits under consideration, because evolutionary change toward the fitness optimum in one trait will also result in a fitness increase in the other traits (Arnold et al. 2001, Guillaume and Whitlock 2007).

We set the off-diagonal elements of ω to 25, a value used in prior studies to simulate weak stabilizing selection (Jones et al. 2003, Guillaume and Whitlock 2007). We then varied the diagonal elements of ω so that r_s varied between 0.25 and 1. An individual's fitness weight determined the probability that it would survive stabilizing selection, which was applied only to fish that had survived to recruitment. Performing selection steps in this order increased model execution speed, because the number of simulated offspring that survived the first year in the

marine environment was far lower than the total number of offspring generated per year.

After determining fitness, the mean reproductive success of immigrants versus non-immigrants was estimated within each population. Here, individual reproductive success was defined as the number of offspring produced that survived freshwater and marine life stages, before passing through the fishery.

Model verification

The model was tested by generating 200 individuals for each population and running them through the sequential stages in the model (Fig. 1). Outputs from each step were checked to ensure that results reflected the desired properties and theoretical expectations for each submodel.

Simulation experiments.—Before starting each set of simulation experiments, the burn-in model was run for 1000 yr with no dispersal between populations, in order to stabilize population trait means and variances. The burn-in simulation used the following parameter values: $h^2 = 0.3$, $r_s = 0.5$, $\mu = 533$ for females and $\mu = 540$ for males, Ricker $\alpha = 2.25$, replacement abundance (S_r) of the stream population = 3000, and S_r of the beach population = 2900. Although the empirical census sizes for A Beach and A Creek are <1000 individuals each, these abundances were used because they resulted in similar numbers of spawners for both populations under the specified parameter values, such that the demographic contributions of dispersal would be similar for both populations. The salmon generated during the burn-in simulations were then used to initialize the simulation replicates. Data on salmon recruits from last 50 yr of the burn-in simulations (years 951–1000) were randomly grouped into 10 blocks of data, with each block containing five years of recruits. Each data block was then used to initialize one of the 10 replicates that were run for each simulation. Each simulation was run for 100 yr.

The first set of simulations tested the evolutionary and demographic effects of the three submodels that applied selection to the simulated populations, namely the size-selective harvest submodel, the predation submodel, and the fitness submodel under stabilizing selection. First, all submodels were retained to simulate a baseline case. For each subsequent simulation (three total), a single, different selection submodel was

removed. The parameter values were the same as those used in the burn-in.

The second set of simulations determined migration–selection balance at varying levels of stabilizing selection and gene flow. For this set, we ran a total of 20 simulations that represented different combinations of stabilizing selection (four levels with r_s ranging from 0.25 to 0.90) and dispersal rates between populations (five levels). Because the numbers of strays relative to the total number of spawners (proportion of strays) within a population ultimately determine the evolutionary effects of straying on that population, we adjusted dispersal rates so that the proportion of strays in each population varied from 0 to 0.20, in increments of 0.05.

Model outputs were averaged over replicates for all simulations. The outputs we focused on specifically were as follows: mean body length and body depth for each sex, proportions of fish belonging to each age class, mean reproductive success (in terms of recruitment) for strays and non-dispersers, and numbers of spawners (individuals that actually mated), after 100 yr had passed. Recruits per spawner and population growth rates (following McClure et al. 2003) were also calculated for each year. We also produced contour plots of mean trait differences between populations to consider evolutionary impacts on phenotypic differentiation.

Sensitivity analysis.—We conducted sensitivity analyses on the parameters (aside from stabilizing selection and dispersal) that were likely to have the greatest potential effects on mean phenotypic trait values and population dynamics. These parameters were heritability (h^2 , used to calculate G), the sex-specific fork length of peak vulnerability to harvest (μ , used in the harvest submodel), and the parameter controlling the shape of the Ricker spawner–recruit function (α , used to determine freshwater and first-year marine survival in the heritability submodel).

Simulations used for sensitivity analyses were initialized using data from a 1000-yr burn-in simulation with no dispersal between populations, $h^2 = 0.3$, $\mu = 533$ for females and $\mu = 540$ for males, and $\alpha = 2.25$. Each parameter was then independently varied ($\pm 10\%$) from the starting value used for the burn-in simulation, and the simulation was run for 100 yr with 10 replicates. The monitored simulation outputs were mean

body length, body depth, proportions of fish belonging to each age class, numbers of spawners, and recruits per spawner after 100 yr had passed. Here, recruits were defined as the number of fish produced that survived to reach the fishery (returns). Outputs were averaged across replicates, and the percent change in each output relative to the baseline case was calculated.

RESULTS

Simulations 1—effects of the different selection submodels

The first set of simulations showed how harvest, predation, and fitness affected trait evolution and population demography. Mean population

trait values were most strongly affected by the harvest and fitness submodels. In the baseline case where all selection submodels were retained, population attributes remained stable for the 100 yr of the simulation (Fig. 2) and were consistent with the values attained during the 1000-yr burn-in simulations. When predation selection on the stream population was removed, mean phenotypic trait values in that population changed only slightly. In contrast, removing harvest selection caused a noticeable shift toward larger body sizes (Fig. 2). Even greater phenotypic changes were observed when stabilizing selection on body size was removed, with decreased mean body sizes for each age class (Fig. 2), presumably because earlier maturation was favored by

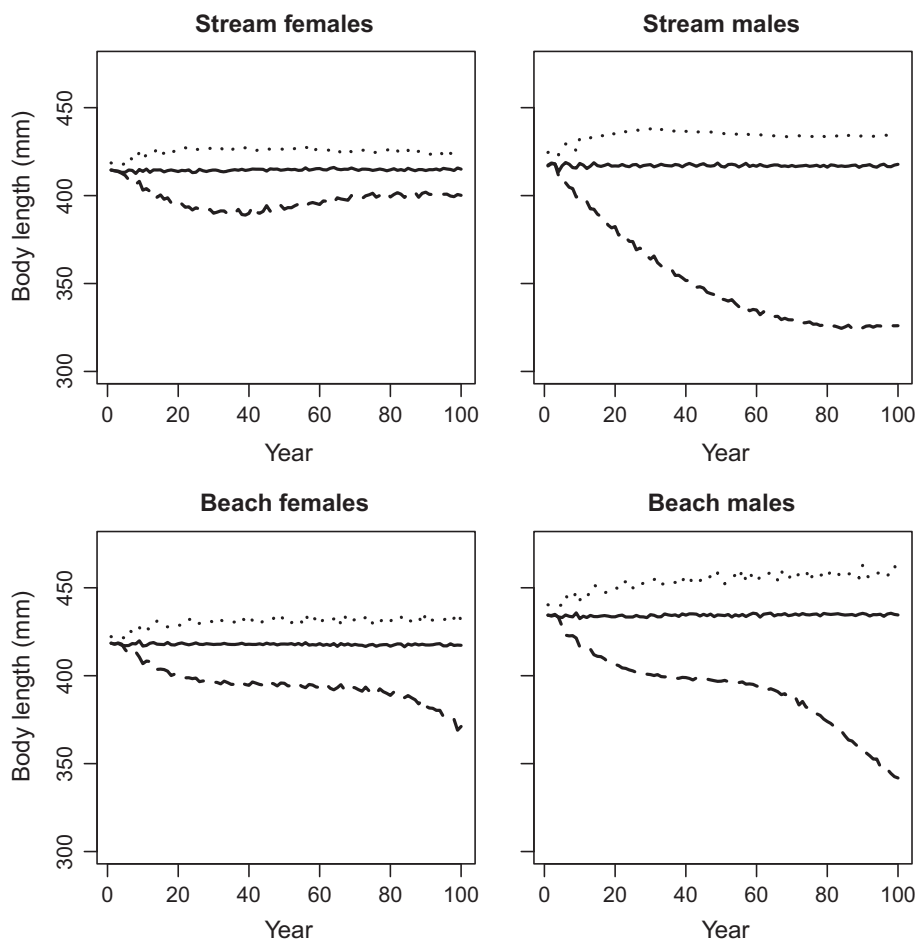


Fig. 2. Mean body length over time for each population and sex, considering scenarios where the effects of different submodels were removed. The solid line represents the baseline scenario, the dotted line represents the scenario when harvest is removed, and the long-dashed line represents the scenario when stabilizing selection is removed. Removing predation selection had very little effect on mean trait values relative to the baseline scenario and was not shown here.

harvest selection and because natural selection was countervailing to harvest-induced selection on body size. Evolution of early maturation was also observed in age structure; the proportion of age-3 individuals increased from about 2% to 62% in the stream population, and from 0.1% to 5% in the beach population after 100 yr. Consequently, the overall mean trait values within each population decreased over time, especially in males (Fig. 2). These results are consistent with the expectation that harvest size selectivity was greater in the stream than in the beach population.

Removing the harvest submodel had the greatest demographic impacts relative to the baseline scenario. When no harvest occurred, median spawner number increased 75% within the stream population and 56% in the beach population (Fig. 3). Removing stabilizing selection on body size slightly reduced spawner numbers in the stream population and slightly increased numbers in the beach population (Fig. 3). Removing bear predation resulted in an increase of about 22% in the median number of stream spawners and about 19% in the number of beach spawners (Fig. 3). Examining the total run sizes (number of individuals surviving freshwater and marine stages but before harvest) and escapements (number of returning adults that escaped harvest) revealed some additional information about the effects of stabilizing selection on demography. Specifically, removal of stabilizing selection on body size led to evolution of smaller body sizes that made the salmon less susceptible to the fishery. For example, with stabilizing selection, harvest removed 61% of returning stream fish and 68% of returning beach fish. Without stabilizing selection, fish evolved smaller body sizes and were less likely to be caught, such that harvest removed 39% of returning stream fish and 38% of returning beach fish. Under both scenarios, beach spawners were more susceptible to harvest than stream spawners due to their larger body sizes overall.

Simulations 2—balance between stabilizing selection and gene flow

The second set of simulations illustrated the different influences that stabilizing selection and dispersal had on trait evolution through migration–selection balance. Both harvest selection on body size ($\mu = 533$ mm for females and $\mu =$

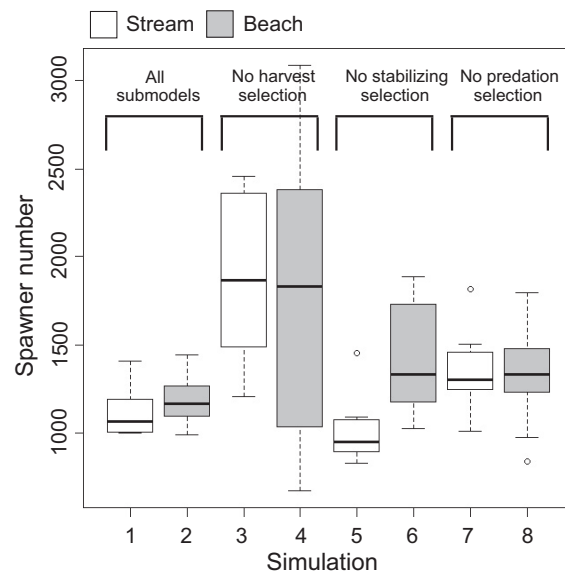


Fig. 3. Boxplots of spawner number for the simulations where different selection submodels were removed. The black line is the median number of spawners at year 100, and the boxes describe the interquartile range over all 10 replicates. Simulations 1 and 2 included all selection submodels (including the predation submodel for the beach population), simulations 3 and 4 had harvest selection removed, simulations 5 and 6 had stabilizing selection removed, and simulations 7 and 8 had predation selection removed. Data for the stream population are in white (odd simulation numbers), and data for the beach population are in gray (even simulation numbers).

540 mm for males) and predation selection were included in these simulations. Harvest rates removed approximately 40–76% of recruits from each population each year (see the capture probability equation above for the model), whereas predation removed about 20–30% of individuals returning to the stream population each year (see the predation probability equation above).

For this set of experiments, we varied dispersal rates and intensity of stabilizing selection on morphology and will focus here on the trait of male body depth, as it differed substantially between ecotypes. When stabilizing selection alone was varied (no dispersal applied), mean male body depth increased with stabilizing selection in both populations (Appendix S1: Fig. S1). When dispersal rates alone were varied (with r_s constant at 0.5), increasing dispersal led to an

increase in mean body depth in the stream population and to a decrease in the beach population (Appendix S1: Fig. S2), making the two populations more phenotypically similar. In terms of age structure, the proportion of age-5 individuals within each population (both sexes) increased with stabilizing selection, whereas proportions of age-3 fish decreased (Appendix S1: Fig. S3). Variation in dispersal rate had minimal effects on age structure (Appendix S1: Fig. S4).

As expected, stabilizing selection on morphology and dispersal had opposing effects on phenotypic differentiation between the two populations, with increasing dispersal reducing phenotypic differentiation and increasing stabilizing selection maintaining that differentiation. The balance of the effects of selection and gene flow on phenotypic differentiation varied, depending on the dispersal rate. At lower dispersal rates (0–0.05), phenotypic differentiation between the two populations was maintained regardless of the level of stabilizing selection, whereas at higher dispersal rates, the strength of stabilizing selection had a greater effect on phenotypic differentiation (Fig. 4). However, these patterns do not relate directly to local adaptation within each population, which always increased with stabilizing selection.

Stabilizing selection on morphology also had greater effects on demography than did dispersal. Spawner numbers decreased in both populations as stabilizing selection increased, as would be

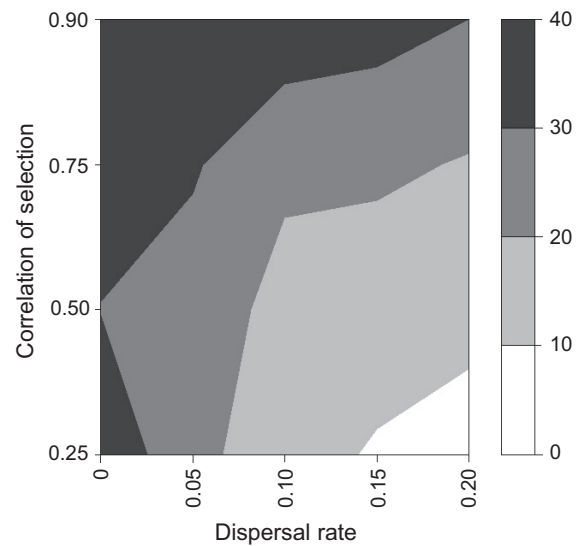


Fig. 4. Contour plot of differences in male body depth at maturity (mm) between the two populations, after 100 yr. The correlation of selection on body length and depth is unitless and relates to the strength of stabilizing selection, and dispersal rate corresponds to the proportion of individuals within each population that disperse.

expected based on results from first set of simulations testing effects of the different selection sub-models (Fig. 2; Appendix S1: Fig. S5). Recruits per spawner generally increased with stabilizing selection (Fig. 5), because the salmon were closer to their population optima and had higher fitness. Density

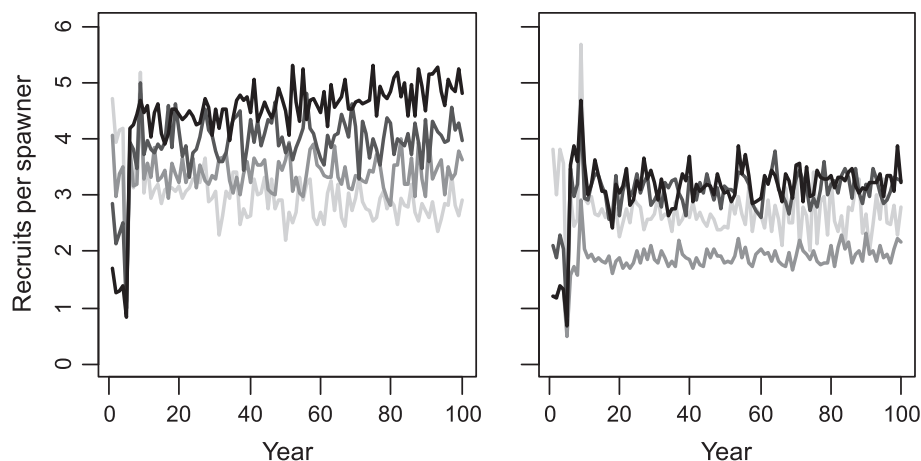


Fig. 5. Recruits per spawner over time in the stream (left) and beach (right) populations. These simulations did not include dispersal and show variation over levels of stabilizing selection (line color becomes darker as the correlation of selection r_s increases).

dependence may also have increased recruits per spawner because population growth rates were fairly constant over time in both populations (Appendix S1: Fig. S6) and the number of spawners decreased with increasing stabilizing selection. Interestingly, recruits per spawner was higher in the beach population when $r_s = 0.25$ than when $r_s = 0.50$. When $r_s = 0.25$, the small size of the fish appears to have increased recruits per spawner because more individuals survived the fishery.

Dispersal had some effects on population growth rates and levels of local adaptation. The relative reproductive success of immigrant males to philopatric males was generally less than one (Appendix S1: Fig. S7). However, relative reproductive success of immigrants increased with dispersal at high levels of stabilizing selection ($r_s \geq 0.5$), especially in the beach population (Appendix S1: Fig. S7), perhaps because

phenotypic differentiation between ecotypes decreased with increasing dispersal.

Sensitivity analysis

Sensitivity analysis revealed that of the tested parameters, changes in μ (body length of peak vulnerability to harvest selection) had the greatest effect on evolution of mean trait values and age structure. For trait values, we focus on results for male body length since patterns for body length and depth were very similar, and phenotypic differences between populations were more pronounced in males than in females. Increasing μ by 10% increased mean body length by about 2% in stream males and 1% in beach males (Fig. 6). Decreasing μ by 10% led to a 3% increase in mean body length in stream males and an 11% increase in beach males (Fig. 6). In terms of age structure, decreasing μ lowered the proportion of age-4

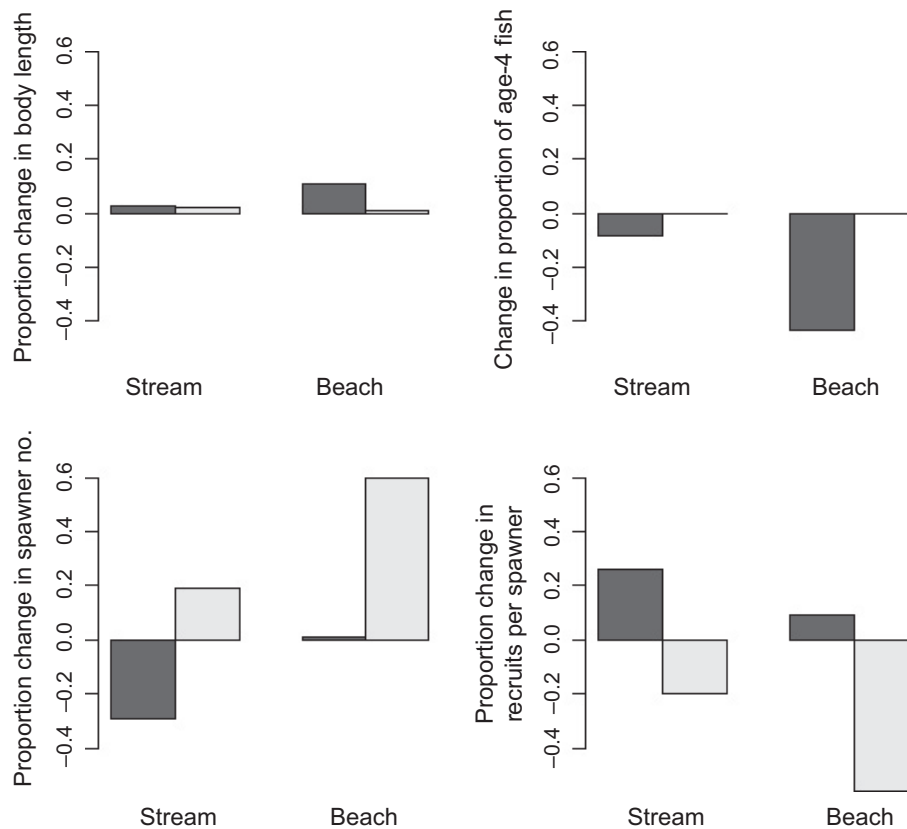


Fig. 6. Sensitivity of mean male body length (top left), proportion of age-4 individuals (top right), spawner number (bottom left), and recruits per spawner (bottom right) in the stream and beach populations to changes in body length of peak vulnerability to harvest (μ). The μ parameter was decreased by 10% (dark gray bars) and increased by 10% (light gray bars) for the analysis.

individuals in the stream population by 8% and in the beach population by 44%, while increasing the proportion of age-5 individuals in both populations. Increasing μ had relatively little impact on age structure. These changes occurred because increasing μ allowed relatively large individuals in both populations to escape the fishery, whereas decreasing μ caused smaller fish within both populations to be caught. Selection on body size and age was stronger in the beach population when decreasing μ , resulting in greater evolutionary change for that population. Changing h^2 and α resulted in less than a 1% change in mean trait values and age structure.

Since spawner numbers and recruits per spawner were especially variable among simulations, data interpretation was somewhat challenging. Nevertheless, μ clearly had the greatest effects on these demographic metrics. Decreasing μ had different effects on the two populations: Spawner numbers in the stream population decreased because a higher proportion of the population became more vulnerable to harvest, whereas spawner numbers in the beach population changed little (Fig. 6). Increasing μ resulted in larger spawner numbers in both populations (Fig. 6) because individual susceptibility to harvest decreased for both populations, especially the beach population. Recruits per spawner had an inverse relationship with μ due to density-dependent effects. For example, harvest mortality decreased when μ increased, and since spawner numbers were higher, carrying capacity limited the number of recruits that each spawner produced. Changing α and h^2 had more ambiguous effects on demography. For both populations, decreasing α decreased spawner numbers, and increasing α increased spawner numbers, an expected result since α affects overall population productivity. However, α did not affect mean recruits per spawner in a clear and consistent manner. Likewise, changes in h^2 for spawner size and age did not result in directionally consistent increases or decreases in spawner number or recruits per spawner, suggesting h^2 had minimal effects on demography.

DISCUSSION

Here, we developed an individual-based, quantitative genetic model to simulate trait evolution

and population dynamics in connected populations of sockeye salmon, and we used the model to determine how opposing selection pressures and varying dispersal rates would affect local adaptation and population sizes. Testing of the selection submodels revealed that size-selective harvest and stabilizing selection influencing spawner fitness—primarily through body size—within subpopulations had substantial and generally opposing effects on mean phenotypic trait values. Harvest selection usually caused fish to evolve smaller body sizes, whereas stabilizing selection favored larger body sizes. In addition, the interaction between harvest and stabilizing selection affected population dynamics, as the larger body sizes favored by stabilizing selection were more susceptible to harvest. We also discovered that modest dispersal between populations did not strongly affect population abundance, even though the resulting gene flow reduced local adaptation. Under the simulation parameters used, it appeared that stabilizing selection had greater overall impacts on trait evolution and population dynamics than did gene flow.

The harvest submodel caused evolution of smaller body sizes at maturation, which is likely due to the influences of two factors. First, younger ages, and consequently smaller sizes, may be favored because fish will have increased fitness if they reproduce before being caught (Dieckmann and Heino 2007). Second, fisheries might target fish within a range of sizes or above a specific size threshold, depending on the types of fishing gear used. In our model, both types of effects were present. When there was harvest selection but no stabilizing selection, the fish matured at very small sizes and young ages, indicating that early maturation was favored due to harvest pressure. As for size selectivity, sensitivity analyses showed that changing the body length of maximum vulnerability to harvest (μ) caused evolution in body sizes within both populations, with size selectivity being stronger in the stream population. For example, increasing μ increased the body size of stream spawners while decreasing the size of beach spawners, with a larger magnitude of evolutionary change in the stream population. Past research on the Bristol Bay sockeye salmon fishery has found that size selectivity can be greater on stream-spawning populations with relatively small salmon, as the larger fish within those

population are more vulnerable to harvest (Kendall and Quinn 2009). Thus, the evolutionary effects of the harvest submodel on body size appear to be realistic.

Stabilizing selection had substantial effects on salmon body sizes as well, countering harvest selection by favoring individuals with trait values close to the population optima (Allendorf and Hard 2009). Other than stabilizing selection, the fecundity and mating submodels were the primary sources of directional selection favoring larger body size: Larger females had greater fecundity, and females preferred mating with larger males. However, these selection pressures were comparatively weak, as they did not compensate for the stabilizing selection when it was removed. In nature, stabilizing selection does not exist as a single unified process; rather, it results from opposing selective forces on a trait, such as temporal variability in selection (Madsen and Shine 1993) or interactions between sexual selection and predation selection (Quinn et al. 2001a). The finding that stabilizing selection was required to maintain reasonably large fish body sizes suggests that there are selective forces operating in nature we did not identify or that our selection models may need further adjustment. For example, offspring of larger individuals may have an additional fitness advantage that we did not capture, such as increased survival during the freshwater stage due to larger egg weight (Quinn et al. 1995). Other potential sources of selection include the likelihood that bear predation varies with body size and depth (e.g., bear predation may be more efficient on deep-bodied phenotypes, which are much more common in the beach-spawning ecotype); differences in migration costs between the ecotypes that also vary with body size; sexual selection among spawners; and selection during the marine phase that might act on ecotypic variation in growth and harvest vulnerability. Our model did not directly address these other sources.

Another important result was that the interaction between stabilizing natural selection and harvest selection affected population dynamics. In our model, increasing stabilizing selection led to the evolution of phenotypes that were more susceptible to harvest, decreasing equilibrium population sizes. Although recruits per spawner increased with increasing stabilizing selection,

population growth rates stayed constant and did not completely counter the demographic effects of increased vulnerability to harvest. There is increasing concern about evolutionary change affecting population dynamics (Saccheri and Hanski 2006, Hutchings and Fraser 2008, Enberg et al. 2009), and our model shows how conflicting selection pressures might have a pronounced effect on demography over ecologically relevant time frames. Harvest selection may especially favor earlier age at maturation in semelparous Pacific salmon, since none of the individuals caught by the fishery have had the opportunity to reproduce. Nevertheless, our results should also apply to iteroparous species, because size-selective harvest can influence body sizes in these species as well, and because multiple episodes of selection on the same cohort may produce a strong response to selection (Eldridge et al. 2010). Our results show how the countervailing processes of selective harvest and of natural selection operate on the key traits of size and age in both stream and beach spawners, as well as their consequences for abundance and productivity of both ecotypes (Fig. 6). They also demonstrate how the populations can sustain their productivity in this complex, linked selective regime through local adaptation mediated by stabilizing selection on body size, especially in stream-spawning fish, at least when dispersal is low (Fig. 5). The sustainability of production of both ecotypes ultimately depends on intact spawning and rearing habitat, stabilizing selection on the size and morphology of adults, and fishing mortality that is neither too high nor too selective over a cohort.

With regard to our original hypothesis, we found that relatively high gene flow reduced local adaptation but did not strongly impact population productivity. One explanation for the lack of detectable effects on productivity in our model is that dispersing females were selected randomly with respect to phenotype and always mated successfully due to the structure of the mating submodel. Since both sexes contributed to the phenotypes of simulated offspring, differences in reproductive success between immigrants and non-immigrants may have been diminished. There was also sufficient phenotypic diversity in the offspring of immigrant parents such that some always survived stabilizing selection. Retention of ample genetic and phenotypic

diversity may ultimately be one of the most important factors for long-term population viability, allowing a population to adapt to environmental change (Saccheri and Hanski 2006, Pelletier et al. 2007).

An additional finding was that the opposing effects of gene flow and stabilizing selection on phenotypic differentiation between populations varied with dispersal rate. When dispersal rates were low ($m < 0.05$), variation in dispersal rate had a greater influence on phenotypic differentiation than did variation in the strength of stabilizing selection. However, under higher dispersal rates ($m > 0.05$), stabilizing selection had a greater impact on phenotypic differentiation. When gene flow was more limited, the impact of stabilizing selection was also minimized because the potential for phenotypic homogenization between populations was lower, and variation in dispersal rates had comparatively greater influence on phenotypic differentiation. In general, our results suggest that the tension that can exist between stabilizing selection to increase fitness in a local population and migration between populations that have different phenotypic optima tends to increase when dispersal rates are higher, unless stabilizing selection is very weak. Regardless, under all investigated scenarios, increasing dispersal resulted in reduced local adaptation. These findings highlight the value of considering evolutionary and demographic processes jointly in investigating the dynamics of populations in the wild (Coulson et al. 2010).

Although the model does provide some interesting results regarding the effects of selection on body size, there are some model components that would benefit from additional refinement. For example, differences in body size between age-4 and age-5 fish were sometimes very small, but demographics may have been the cause. The proportions of age-4 fish were much greater than those of age-5 fish, especially at the highest intensity of stabilizing selection, and thus, selection may have been most effective on that age group. More importantly, it would be useful to design a model that does not require stabilizing selection to produce realistic fish body sizes, as we would then likely have a better understanding of the selection pressures that operate in nature.

Because the model is designed to be very flexible, it should lend itself to testing other

hypotheses. For instance, determining the extent to which phenotype-biased dispersal affects local adaptation and differentiation is an important question that previous research has found evidence for in sockeye salmon (Lin et al. 2008). In theory, adaptive divergence will increase when there is selection against phenotypically distinct immigrants (Hendry 2004, Garant et al. 2007), but variation in selection intensity as well as the phenotypes of potential immigrants may influence evolutionary outcomes. Another potential extension of the model is to determine how variation in harvest selection over time may affect trait evolution and population sizes, as environmental heterogeneity can affect genetic variance and hence evolutionary dynamics (Kruuk and Hill 2008). In sockeye salmon specifically, fishery selection differentials can vary substantially each year (Kendall et al. 2009), which may have different evolutionary consequences than consistent selection for a specific and narrow range of body sizes.

CONCLUSION

Our study simulated the evolution of correlated phenotypic traits affecting reproductive fitness in wild sockeye salmon populations connected by dispersal and illustrated the effects of different types of selection as well as the interaction between gene flow and local adaptation on trait evolution and population demography. We found that dispersal reduced local adaptation but did not strongly affect population productivity; the effects of migration–selection balance on phenotypic differentiation depended on the dispersal rate. Although we did not observe strong direct impacts of gene flow on reduction of sockeye salmon population productivity, the model demonstrated that evolutionary change can have appreciable demographic consequences over ecologically relevant time scales, which has important implications for selective fisheries and large-scale environmental forces that can impose selection to alter or constrain phenotypic variation to cope with such changes.

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DATA AVAILABILITY

The phenotypic and microsatellite data used for pedigree reconstruction and to parameterize the models are stored on Dryad under <https://doi.org/10.5061/dryad.b46qg>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2039/full>