Microevolution, local adaptation, and demography in wild populations of Pacific salmon

Jocelyn Lin

A dissertation
submitted in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

University of Washington
2012

Reading Committee:
Lorenz Hauser, Chair
Ray Hilborn
Jeffrey Hard

Program Authorized to Offer Degree:
School of Aquatic and Fishery Sciences

University of Washington

Abstract

Microevolution, local adaptation, and demography in wild populations of Pacific salmon

Jocelyn Lin

Chairs of the Supervisory Committee:
Associate Professor Lorenz Hauser
Professor Ray Hilborn
School of Aquatic and Fishery Sciences

There is increasing scientific interest in empirically linking evolution to ecology, particularly in wild populations. Although evolutionary change is often thought to proceed slowly, the microevolutionary forces of selection, gene flow, genetic drift and inbreeding can have pronounced effects on genetic variation even on short time scales. These genetic changes may then influence local adaptation and demography. The overarching aim of this dissertation was to estimate levels of gene flow and selection in wild populations, and to assess how microevolutionary change might affect local adaptation and population dynamics within these populations.

Pacific salmon (*Oncorhynchus* spp.) are an ideal model organism for studying natural patterns of microevolution and local adaptation. First there is high phenotypic variation within the species, and spawning fish can be sampled comprehensively by capturing adults when they return to freshwater from the ocean. Second, salmon form

reproductively isolated spawning populations due to natal homing, but these populations can be genetically and demographically connected via straying. Third, salmon are of ecological and commercial interest, making our findings relevant to population management.

This dissertation investigated ecology and evolution in salmon as follows. In Chapter 1, we examined patterns of genetic and phenotypic differentiation between adjacent populations of beach and stream spawning ecotypes of sockeye salmon, and assessed potential levels of gene flow between ecotypes. The objective of Chapter 2 was to determine whether small populations of Chinook and chum salmon occurring in the Wood River system are reproductively isolated, self-sustaining populations, population sinks that produce returning adults but receive immigration, or strays from other systems that do not produce returning adults. In Chapter 3 we re-constructed pedigrees for two wild populations of sockeye salmon to estimate natural selection and heritability for several phenotypic traits. For Chapter 4, we used empirical results from the first three chapters to develop a stochastic, individual-based model that we used to study effects of gene flow and selection on local adaptation and population dynamics in interconnected salmon populations. Taken together, these studies showed how gene flow and selection affect local adaptation and demography in wild salmon populations.

Table of Contents

List of Figures

Figure Number Page

List of Tables

Table Number Page

Acknowledgments

Many people have helped me complete this dissertation. My supervisory committee, headed by Lorenz Hauser and Ray Hilborn, has provided excellent academic and personal guidance. Lorenz and Ray helped me develop great research questions and have taught me much about science in general. Jeff Hard and Tom Quinn have always been extremely generous with their knowledge and moral support, and Willie Swanson has been a fantastic GSR. I would also like to mention that Kerry Naish has been like an extra committee member, providing much helpful advice and encouragement.

I am also very grateful for my colleagues at the University of Washington. The students in MERLab, both past and present, have been a fantastic lab group: thanks to Todd Seamons, Willy Eldridge, Erin McClelland, James Franks, Carl Osterberg, Piper Schwenke, Maureen Hess, Miyako Kodama, Marine Brieuc, Shannon O'Brien, Teresa Sjostrom, Dan Drinan, Charlie Waters, and Daniel Peterson. Our lab technicians, Lyndsay Newton, Melissa Baird, and Isadora Jimenez, kept our lab functioning smoothly and also helped run the genetic data. From the Alaska Salmon Program, I particularly thank Chris Boatright, Jackie Carter, Daniel Schindler, Richie Rich, Peter Lisi, Jonny Armstrong, Anne Hilborn, Ulrike Hilborn, Katy Doctor, and Rachel Hovel for their assistance with collecting field and survey data. Being able to conduct research in Alaska was an amazing experience, and I couldn't have done it without them. I also received

support from other SAFS lab groups, and special mentions go to Carey McGilliard, Allan Hicks, Curry Cunningham, and Kotaro Ono in the Hilborn lab, and Joe Anderson, Stephanie Carlson, Neala Kendall, George Pess, Peter Westley, and Pam Woods in the Quinn lab.

Several members of federal agencies (USGS, ADF&G) generously contributed samples and data, which greatly strengthened my research projects. Special thanks go to Jeffrey Olsen, Chris Habicht, Gregory Buck, and Michael Wiedmer. Ryan Nielson at West Inc. provided extensive code and help with the salmon population model.

For financial support, I thank the National Science Foundation, the NMFS-Sea Grant Population Dynamics Fellowship, and SAFS. I would also like to express my gratitude to the administrative staff at the School of Aquatic and Fishery Sciences, particularly Scott Schafer, Robin Weigel, Jessica Roshan, and Addi Daisley, for helping me navigate graduate school.

Finally, I have received wonderful emotional support from my friends and family. My parents, Jim and Sunny Lin, have cheered me on the entire way. Max Lin, Katherine Chou, Ellen Lin, Rhonda Morales, Danielle Mitchell have always been there for me when I needed them. I also want to thank Greg Drugan, who is a fantastic partner in so many ways. Thanks to all of you!

General Introduction

Patterns of genetic and phenotypic diversity reflect the evolutionary past of a species as well as its future evolutionary potential, and thus studying these patterns in wild populations can improve ecological knowledge and contribute to effective population management. Impacts of demography on evolution have long been recognized, but the effects of evolution on species ecology have not. Indeed, there is increasing scientific interest in empirically linking evolution to ecology, as recent studies have demonstrated that evolution can affect demography even on relatively short time scales (Kinnison *et al.* 2007). In particular, reduction of local adaptation may decrease population sizes.

Despite the growing recognition that evolution can affect demography, population genetics and population dynamics are rarely explicitly and quantitatively linked in empirical studies (Hard 1995; Naish & Hard 2008). Microevolution (evolution within and among populations due to gene flow, genetic drift, mutation, and selection) determines intraspecific genetic variation and hence affects local adaptation and population sizes. Gene flow homogenizes allele frequencies between populations (Wright 1931), but may also introduce genetic variation, particularly to small populations (Garant *et al.* 2007). Genetic drift is the random fluctuation of allele frequencies, and it affects small populations more strongly (e.g. Waples 1990), potentially leading to loss of genetic variability. Mutation creates genetic variation, which can be adaptive or non-adaptive. Selection on available genetic variation favors adaptive changes. These

microevolutionary forces can interact in complex ways, and better understanding of their combined effects on local adaptation will strengthen our ability to link evolution to demography.

Pacific salmon (*Oncorhynchus* spp.) in particular are an excellent taxon for researching the effects of microevolution on genetic and phenotypic diversity. Some species, notably sockeye salmon (*Oncorhynchus nerka*) and Chinook salmon (*Oncorhynchus tshawytscha*), show extensive variation in life history and morphology (Groot & Margolis 1991; Quinn 2005). Genetic diversity among populations can be high as well, because salmon have a strong tendency to home to natal sites for spawning, and the resulting reproductive isolation can cause these spawning populations to diverge both genetically and phenotypically over time (Waples 1991). On the other hand, salmon also stray, or disperse to non-natal sites to spawn (Quinn 1984), which leads to gene flow among populations. The interplay between straying and homing is key to balancing dispersal ability with the benefits of local adaptation (Hendry *et al.* 2004b; Quinn 1999).

For this dissertation, we examined how microevolution contributes to intraspecific variation, local adaptation, and productivity in Pacific salmon populations. We focused on wild populations spawning in the Wood River Lakes system in southwest Alaska, an excellent study system because the life history and ecology of its sockeye salmon populations have already been well characterized (Quinn *et al.* 2001b). Importantly, the Wood River Lakes are free of hatchery impacts and can therefore provide information on how these micorevolutionary forces operate under natural conditions, although the populations are subject to anthropogenic harvest. There is also indication that life history

variation sustains productivity in the larger Bristol Bay stock complex that includes the Wood River system (Hilborn *et al.* 2003), and thus investigating how such variation arises is useful from a management perspective.

We specifically studied the roles of selection, genetic drift and gene flow in causing patterns of genetic and phenotypic differentiation in these wild salmon populations (Chapters 1 and 2). We also conducted parentage analysis in two of our study populations to determine effects of predation selection and to estimate quantitative genetic parameters (Chapter 3). Finally, using these empirical data, we modeled aspects of microevolution in connected populations of Pacific salmon to see how they may contribute to those populations' abilities to adapt and persist (Chapter 4). Together, these studies contribute to the growing body of research on demographic impacts of evolutionary change.

Chapter 1: Phenotypic and genetic differentiation between beach and stream spawning ecotypes of sockeye salmon (*Oncorhynchus nerka*)

Abstract

Phenotypic and genetic divergence among conspecific populations is driven by many ecological and evolutionary forces. In particular, the antagonistic interaction between local adaptation and gene flow may determine patterns of phenotypic divergence observed in the wild, although the relative strength of the two forces can be difficult to ascertain. For this study, our goals were twofold. First, we examined patterns of genetic differentiation between neighboring, wild populations of beach and stream spawning ecotypes of sockeye salmon (*Oncorhynchus nerka*) and related that differentiation to various environmental factors and the extent of phenotypic divergence. Second, we assessed whether adaptive divergence constrained gene flow between ecotypes, or whether gene flow constrained adaptive divergence. Significant genetic differentiation between ecotypes (F_{ST} = 0.007-0.0479, based on 12 DNA microsatellite loci) was found at locations with a relatively shallow stream, lower heterozygosity, and more pronounced morphological differentiation between ecotypes, especially in males. In contrast, more gene flow was indicated between beach spawning populations and stream spawning populations in deeper streams, resulting in reduced genetic and phenotypic differentiation. Simulations using an individual-based, quantitative genetic model indicated that gene flow can rapidly homogenize phenotypes, but that strong selection

against immigrants can maintain local adaptation, even if some gene flow occurs. Thus in our system, divergent selection appears to have a strong impact on at least some of our ecotype population-pairs, especially the ones that are very phenotypically divergent but not very genetically differentiated.

Introduction

The evolution and maintenance of genetic and phenotypic diversity in wild populations is a central topic in both ecology and evolution because such diversity not only determines species abundance and distribution but also leads to local adaptation and eventual speciation. The forces involved in these natural processes are well established in theory, but empirical evidence is scant. For example, although the effect of genetic drift is well established for neutral molecular markers, its effect on phenotypic divergence is less clear (Koskinen *et al.* 2002). More importantly, although the antagonistic effects of gene flow and local adaptation are understood theoretically and have been described empirically, the causal relationship between the two forces is difficult to establish except in some specific systems. For instance, gene flow restricts local adaptation in sticklebacks (Moore *et al.* 2007), and local adaptation may prevent gene flow by limiting reproductive success of migrants (Hendry *et al.* 2007). However, the general applicability of such results is uncertain, especially with respect to features of the physical environment, and additional empirical studies are needed.

Wild sockeye salmon (*Oncorhynchus nerka*) are an ideal model organism for studying such interactions between different evolutionary forces. Homing to natal sites for reproduction leads to well defined populations, which experience only limited gene

flow and display considerable phenotypic divergence in morphology and life history. For example, reproductive ecotypes of sockeye salmon utilize different spawning habitats, notably streams flowing into lakes, and lake beaches oxygenated by ground water flow (Quinn 2005). The two ecotypes show striking morphological differences; beach males are typically much deeper-bodied than stream males, likely as a result of both natural and sexual selection. Beach sites are easy to access regardless of body shape, and fish at those sites are largely safe from bear predation, allowing sexual selection to favor large, deep-bodied males (Blair *et al.* 1993; Quinn & Foote 1994). Stream males, on the other hand, are often exposed to higher predation and stranding risk, both of which select against large, deep-bodied fish (Quinn *et al.* 2001a). The same trade-off may act within stream spawners, as deeper streams often have deeper-bodied fish than shallower streams (Quinn *et al.* 2001b).

Previous research has found varying levels of genetic differentiation within and between ecotypes within the same watershed. Differentiation among nearby stream spawning populations can be minimal or high (Lin *et al.* 2008a; Lin *et al.* 2008b), but differentiation among beach spawner populations is generally low, suggesting the presence of metapopulations with considerable levels of gene flow (Gomez-Uchida *et al.* 2011; Lin *et al.* 2008a). Beach and stream populations are sometimes genetically distinct, especially within lakes or on finer-geographic scales (Gomez-Uchida *et al.* 2011; Lin *et al.* 2008a). However, none of these prior studies specifically focused on the relationship between dispersal and population differentiation in relation to habitat conditions. Some beach and stream spawners occur in close proximity, which effectively removes

geographic barriers to dispersal. Specifically, salmon spawn in streams and also in lake beaches only tens or hundreds of meters away, with no physical barrier to movement between habitats. Such population-pairs of beach and stream spawners occur at multiple sites within Bristol Bay lake systems, providing opportunities to study the interaction between local adaptation and gene flow.

Here, we address the question of the relationship between local adaptation and gene flow by quantifying genetic and phenotypic divergence in nine beach-stream ecotype population pairs of sockeye salmon spawning in close geographic proximity in the Wood River and Iliamna systems in Alaska, USA. First, we estimate the effects of habitat features, in particular stream depth, width and length, on phenotypic and genetic differentiation between stream and beach spawners. Second, we determine how gene flow might affect phenotypic divergence, and conversely, whether specific levels of divergence might constrain gene flow by simulating trait evolution in connected sockeye salmon populations.

Materials and methods

Study sites and survey data

Nine pairs of beach-creek populations in the Wood River and Iliamna Lake systems, Bristol Bay, Alaska (Figs. 1.1, 1.2) were sampled. Pairs were used because experimental designs involving paired population sites tend to increase accuracy in detecting the effect of landscape on dispersal, particularly for scenarios where direct dispersal occurs mostly between adjacent populations (Jaquiery *et al.* 2011). Within each

pair, the beach spawning population was located less than 800 m from the stream spawning population, with one exception (Pick Creek/N6 Beach), where the beach and stream sites were ca. 3 km apart. Wetted length, depth, and width measurements were taken of all streams, but physical habitat differences among beaches were not quantified due to the difficulty of defining standardized measures for beach habitat that had limited accessibility. Distances between sites (measured as the shortest distance in water) were calculated using GPS coordinates and Google Earth 2007. Stream measurements, including length, wetted depth, and wetted width (Table 1.1) were taken by the staff of the Fisheries Research Institute of the University of Washington (FRI), and US Fish and Wildlife Service (Demory *et al.* 1964; Quinn *et al.* 2001b).

Fish counts from survey data were used to estimate census population sizes within each stream. In the Wood River system, FRI has conducted surveys on foot, where crews of three or more people enumerated live, senescent, and bear-killed fish at least once during the spawning season. The Wood River surveys took place from 1946 to the present, and all streams had at least ten years of surveys, except N4 Creek, which had one survey. Knutson Creek in the Iliamna Lake system has not been surveyed by FRI, but stream counts were obtained from annual aerial surveys conducted by the Alaska Department of Fish and Game from 1956 to 2004. The beach spawning populations in the Wood River system were not enumerated quantitatively, but direct observations were used to compare the relative sizes of the beach and stream populations at each site.

Total spawning population sizes in the Wood River streams were estimated from stream surveys using methods described in Quinn et al. (2003). Over the duration of a

spawning season, the ratio of live fish to total fish (live plus dead) within a stream decreases over time. Data from an extensively monitored stream (Hansen Creek) within the Wood River system suggested that when the ratio of live to total fish was approximately 0.5, the total count that day roughly corresponded to 75% of the total spawning population size over the entire spawning season (Quinn *et al.* 2003). Similar data were also available for two of the populations included in this study; when the ratio of live to total fish was 0.5, A and C creeks contained 39% and 86% of their total population sizes, respectively. Averaging data from all three streams, the mean percentage of the total population size counted at peak spawning was 67%. Thus, the total population size of most streams was estimated as 149% (1/0.67) of counts from surveys where the ratio of live to total fish was 0.4-0.6. In A and C creeks, the total number of spawners counted that season was used instead. The harmonic mean of the estimated spawning population sizes was then calculated over years within each stream, to obtain indices of effective population sizes.

Morphological analysis

Morphological measurements of the fish were obtained from dedicated sampling trips for this study as well as past projects conducted by FRI. Sampling years ranged from 1990 to 2010, and the number of years each population was sampled varied from one to 18 years. At least 100 individuals were sampled from each beach and stream site, and sex, body length, and body depth measurements were recorded to the nearest mm for each fish. Body length was measured from the mid-eye to the hypural plate, and body depth was measured from the anterior insertion of the dorsal fin to the belly,

perpendicular to the long axis of the fish (following Blair *et al.* 1993). Because body length and body depth are highly correlated, body depth measurements were also standardized to a common body length of 450 mm (following Ihssen 1981) to consider differences in body depth independent of allometric growth. The length of 450 was chosen because it approximates the long-term average over all populations and was used in previous research, thereby facilitating comparisons across studies (Blair *et al.* 1993; Quinn *et al.* 2001b). In addition, standardized body shape is more consistent among years than body length, which varies from year to year largely due to variation in age composition (Quinn et al. 2001b, and additional unpublished data).

Phenotypic trait differences between ecotypes within sampling locations were tested using analysis of variance (ANOVA), with sexes analyzed separately due to sexual dimorphism. ANOVA was also used to estimate effect sizes of site, sampling year, ecotype, and the interaction between site and ecotype on body size, which were used to calculate mean trait values that included these effects.

Genetic analysis

Approximately 1 cm^2 of fin tissue was collected from each sampled individual and stored in 95% ethanol (Table 1.2), and 45 to 48 individuals from each site were used in the genetic analysis. DNA was extracted from the fin tissues using Qiagen DNeasy kits (QIAGEN, Valencia, CA, USA), following the manufacturer's protocols. A total of twelve microsatellite loci were used to analyze genetic variation (11 tetranucleotide repeat loci and one dinucleotide repeat locus): *One100*, *One102*, *One103*, *One108*, *One109*, *One112*, *One114* (Olsen *et al.* 2000), *One110c* (J Seeb, personal communication, F: 5'-

GAGTGGCCGTCGTTTTACCCTCCATTTCAATCTCATCC-3' and R: 5'-GCGCATGGTCATAGCTGTTACAGAGAACAGTGAGGGAGC -3'), *Ots3* (Banks *et al.* 1999), *OtsG68* (Williamson *et al.* 2002), *Ots103* (Beacham *et al.* 1998), and *Ots107* (Nelson & Beacham 1999). Each polymerase chain reaction (PCR) included 2µl of a 1:4 dilution of the extracted DNA in low TE, 1.5mM $MgCl_2$, 1mM dNTPs, 2µM of each primer, 1x GeneChoice buffer and 0.5 Units GeneChoice Taq DNA polymerase to make up a total 10µl reaction volume. A touchdown PCR was applied, with 6 cycles of 1-min at 95ºC, 30-sec at (T_{anneal} + 5) °C (-1 °C /cycle), and 15-sec at 72 °C (15s); followed by 22 cycles with the annealing step at T_{anneal}, and a final extension time of 20 min at 72ºC. T_{anneal} stands for annealing temperature and is provided in the primer references except for *One110c* (T_{anneal} = 56 °C, J. Seeb, pers. comm.). All forward primers were labeled with fluorescent dye, and the labeled PCR fragments were size-separated on an automated DNA sequencer (Megabace 1000, Amersham Biosciences) with appropriate size standards. Allele fragment sizes were estimated using Genetic Profiler genotyping software (v2.2, Amersham Biosciences). MICROCHECKER (van Oosterhout *et al.* 2004) was used to check for evidence of null alleles or genotyping error due to stuttering.

Genotype frequencies were tested for departures from Hardy-Weinberg equilibrium and linkage equilibrium with GENEPOP 3.3 (Raymond & Rousset 1995), based on Guo and Thompson (1992). Multi-locus estimates of observed and expected heterozygosity, F_{IS} inbreeding coefficients (Weir & Cockerham 1984), and number of effective alleles were calculated in GENALEX (Peakall & Smouse 2006). Allelic richness, pairwise F_{ST} values between populations (Weir & Cockerham 1984), and statistical

significance of the F_{ST} values were calculated in FSTAT (Goudet 1995). Nei's measure of genetic differentiation G_{ST} (Nei 1973) was also calculated in GENALEX to obtain non-negative differentiation estimates. A multidimensional scaling plot was created to visualize genetic differentiation (F_{ST}) among populations, using SPSS (v. 11.0.1, IBM, Chicago, IL, U.S.A.). Analysis of molecular variance (AMOVA) in Arlequin 3.11 (Excoffier & Lischer 2010) tested whether sampled populations clustered by lake or by ecotype.

Mantel tests in PopTools (Hood 2002) were used to test for isolation by distance with 1000 permutations. LDNE (Waples & Do 2008) was used to estimate effective population sizes (N_e) based on levels of linkage disequilibrium in the samples, assuming a minimum allele frequency of 0.02. The program BIMr (Faubet & Gaggiotti 2008) was used to estimate recent dispersal rates between beach and stream populations at each site, using a generalized linear model and Markov Chain Monte Carlo methods. The burn-in and sample size for estimating the posterior were both set for 10000 iterations. Data from each ecotype pair were run ten times in BIMr, and migration rate estimates from the run with the lowest Bayesian deviance were used, following Faubet et al. (2007).

Effects of landscape, phenotypic, and demographic factors on genetic differentiation

Information theoretic model selection was used to assess factors contributing to genetic differentiation between ecotypes within sites, following methods used in landscape genetics analysis (e.g. Selkoe *et al.* 2010). We focused on factors with hypothesized biological effects on genetic differentiation between ecotypes, namely

stream depth, sex-specific differences in mean body length and body depth (both absolute and standardized) between the beach and the stream populations, and heterozygosity (mean expected heterozygosity of the beach and stream populations at a site). Stream depth and fish body size may affect dispersal and hence gene flow between stream and beach habitats, as large-bodied fish have reduced mobility and increased mortality in shallow streams (Carlson & Quinn 2007). Body size may have especially pronounced effects on dispersal in males because they are larger and deeper-bodied than females (Quinn & Buck 2001). Expected heterozygosity was used as a long term indicator of effective population size, which may affect estimates of genetic divergence.

We calculated two measures of differentiation for each fish morphological trait because sampling was unbalanced among sites, particularly in the number of years each site was sampled. First, we simply subtracted trait means in the stream population from trait means in the beach population. Second, we repeated this process but used mean trait values predicted from ANOVA effect sizes. These mean trait values estimated from ANOVA summarized the phenotypic data while accounting for sampling year, ecotype, site, and ecotype by site effects. Normality of each factor was assessed using Q-Q plots, and correlations between all factors were tested using linear regression models.

All factors were used as single predictor variables in linear regression models that represented different hypotheses about the genetic differentiation between beach and stream populations at specific sites. Since there were only nine population pairs and hence limited degrees of freedom, we did not perform regressions using combinations of predictor variables. Logit-transformed G_{ST} values (Nei 1973) were used as the dependent

variable. Because G_{ST} values are proportions, logit transformations linearize the relationship between G_{ST} and the predictor variables (Cramer 2003). Weir and Cockerham's (1984) estimator of F_{ST} could not be used because the negative estimates could not be transformed. Data from each ecotype population pair were assumed independent, as genetic and geographic data showed no obvious trends among sites. Factors that showed a significant correlation with the dependent variable were then used in model testing, as blindly testing all possible combinations of predictor variables could lead to positive results by chance, especially considering the small sample size (Burnham & Anderson 2002). Weighted model averaging based on Akaike's information criterion corrected for small sample size (AIC_C; Hurvich & Tsai 1993) was used to determine how informative each of the candidate models were.

Relationship between gene flow and selection

Although the linear regression models provided information on the factors associated with genetic differentiation between ecotypes, the relative importance of gene flow and adaptive divergence in determining observed patterns could not be assessed empirically. Thus, we used an individual-based modeling approach to investigate how the interaction between gene flow and selection can shape phenotypic distributions within ecotype populations. Specifically, we simulated beach and stream sockeye salmon populations, varied dispersal rates between the populations as well as the strength of stabilizing selection within each population, and observed the effects on phenotype distributions. Stabilizing selection favors specific trait values within each population and therefore selects against immigrants with phenotypes that deviate from the population

optimum. Dispersal rate and strength of selection therefore determine the influence of gene flow on the population receiving immigrants.

We ran simulations in an individual-based salmon life-cycle model programmed in R (v. 2.12.2, R Development Core Team 2011), described in more detail in Chapter 4 of this dissertation. Briefly, the model simulated multiple populations of individuals with a full salmonid life cycle and specifically tracked individual body length, body depth and age at maturity. When the populations were initialized, the trait values of the salmon were drawn from distributions with means and variances specified by the user. The salmon then underwent harvest, and, in the stream population, predation against larger-bodied individuals. Surviving individuals then mated, with each female spawning and choosing a single male mate. Females preferred males with body lengths at least as large as their own. Female fecundity determined the number of offspring produced per mating, and offspring traits were determined using a multivariate, quantitative genetic model. Specifically, the offspring phenotypes were based on parental breeding values, family-specific genetic deviations, and environmental deviations (Roff 2010; Tufto 2010). Stabilizing selection was then applied to the offspring, such that individuals with trait values deviating from the local population optimum were less likely to survive pre-harvest freshwater and marine life stages. The offspring subsequently underwent harvest selection, completing the life cycle.

For this study, we simulated two morphologically distinct populations of sockeye salmon using empirical body length, body depth, and age data from A beach and creek. We used data from these populations because they show high phenotypic differentiation,

and because we had empirical estimates of heritability for body length and body depth at maturity (mean $h^2 = 0.2$; confidence interval = (0.08, 0.76)) from A Creek. These two simulated populations will be termed the local stream and beach population. To mimic connectivity among beach populations (Lin *et al.* 2008a) maintaining beach phenotypes despite immigration from streams, we also simulated a 'global' beach population that exchanged individuals with the local beach population but not the stream population, expecting that ongoing gene flow would maintain phenotypes in the local beach population.

Parameter values used to determine fish trait values and the local population optima are shown in Table 1.3. Trait means and variances stabilized after a 1000 year model burn-in, with no dispersal among populations. After stabilization, the annual number of spawners was roughly 1000-1500 in each of the three populations. We then varied dispersal rates, defined as the proportion of individuals within one population moving to another population per year, as well as the strength of stabilizing selection within each population. Because the number of spawners was similar for the local stream and beach populations, these dispersal rates were also approximately equivalent to the proportion of each population consisting of strays (treating only individuals that switched spawning habitats as strays). Bi-directional dispersal rates between the local beach and stream populations were varied from 0 to 0.2, covering the approximate range of reported straying levels for Pacific salmon (Hendry *et al.* 2004b) as well as most of the dispersal rates estimated by BIMr. The dispersal rate from the global to the local beach population was held constant at 0.4.

The strength of stabilizing selection was determined by the matrix ω, which describes the curvature and orientation of a Gaussian fitness peak on the adaptive landscape (Lande 1979). The diagonal elements of ω describe variance of the multivariate fitness surface, with larger values result in weaker stabilizing selection. We varied those diagonal elements from 25.1-100 while holding orientation of the selection surface (described by the off-diagonal values of ω) constant at 25. The correlation of selection, which is calculated as $r_s = \omega_{12} / \sqrt{\omega_{11}\omega_{22}}$ in the bivariate case (Guillaume & Whitlock 2007), therefore varied from 0.25 to 1.0. When the correlation of selection is higher, stabilizing selection for a specific optimum phenotype is more effective, and individuals with phenotypes differing from that optimum have lower fitness. As an example from our simulation, at a dispersal rate of 0.1, the relative reproductive success of immigrant males was 0.84 when r_s=0.25 and 0.22 when r_s=1.0. The relationship between phenotype and individual relative fitness at different r_s levels is also shown in Figure 1.3. For example, if the optimum body length is 440 mm, an individual with a body length of 480 mm will have a relative fitness of 0.91 when r_s=0.25, and a relative fitness of 0.51 when r_s=0.75 (Fig. 1.2). For this study, r_s was used to describe the strength of stabilizing selection.

Each simulation was run for 100 years with 10 replicates, and phenotypic trait means were compared between ecotypes. To determine how adaptive divergence might limit gene flow, we estimated relative reproductive success of migrants to non-migrants. Reproductive success was measured as the number of offspring produced per individual that survived freshwater and marine life stages, before undergoing harvest.

Results

Sampling site characteristics

Physical stream characteristics varied substantially among sites. A, C, and N4 creeks were the shortest and shallowest streams, whereas Knutson and Pick creeks were the deepest and relatively long (Table 1.1). Elva Creek was a short but relatively deep stream, and Hidden Lake Creek was a long but relatively shallow stream. Yako and Lynx creeks were moderate in terms of stream length and depth. As might be expected from the reduced available spawning habitat, the shorter streams (A, C, Elva, and N4) supported smaller populations that averaged fewer than 500 spawning sockeye salmon per year, whereas the longer streams averaged over 1500 spawners per year (Table 1.1). Spawners were not specifically enumerated for beach sites, but field observations indicated that the Elva, Anvil Bay, N4, and Knutson beach populations were generally larger than their neighboring stream populations (Table 1.1).

Morphological analysis

ANOVA indicated that fish morphology differed by site, ecotype, and sampling year. There was also a significant ecotype by site interaction, suggesting that the body sizes of the different ecotypes varied by site. Overall, stream fish were shorter and relatively shallow-bodied compared to beach fish, more so in males than in females (Table 1.2). Of the phenotypic traits considered, absolute male body depth showed the most pronounced differentiation between ecotypes, as stream males were approximately 36 mm shallower than beach males across all populations and sampling years (t = -21.0, $P < 0.001$). The sites with the greatest differences in mean male body depth between

ecotypes were Anvil/Hidden and N4, whereas the sites with the smallest differences were N6/Pick and Knutson (Table 1.2).

Genetic analysis

Six of 18 populations (Elva Beach, Hidden Lake Creek, N4 Creek, Knutson Beach, Knutson Creek, Yako Creek) showed an overall significant departure from Hardy-Weinberg equilibrium based on exact tests for heterozygote deficiency in GENEPOP (Table 1.4). For these six samples, significance appeared largely driven by one locus, *One*100 (Table 1.S1). MICROCHECKER suggested the presence of a null allele at that locus, but because excluding the locus did not change overall results (data not shown), we retained it in the analysis. Pairwise linkage disequilibria occurred with greater than expected frequency (0.05; four or more of 66 tests) in 13 out of the 18 samples. The only samples that showed < 5% linkage disequilibrium were those from A Beach, Anvil Bay Beach, Hidden Creek, N4 Beach, and Yako Beach. Samples from C beach and creek showed especially high occurrences of linkage, with 44% and 36% of pairwise comparisons between loci being significantly out of linkage equilibrium, respectively. High levels of linkage may indicate physical linkage between loci, population mixing between genetically differentiated populations, low effective population size (N_e), or sampling of related individuals. Other studies have found no evidence of physical linkage in the loci used (Olsen *et al.* 2004), and permutation tests of mean relatedness within populations (IDENTIX; Belkhir) did not show higher than expected relatedness within any of the samples. Thus, the more probable contributors to the observed linkage were small effective population sizes or population mixing. Indeed, most N_e estimates were fairly

low (Table 1.4), and in a previous study on the A and C populations, linkage was completely explained by low N_e (Lin *et al.* 2008a). As significant linkage was not consistently associated with specific pairs of loci, however, no loci were excluded on the basis of linkage.

Summary genetic measures (Table 1.4) indicated that the beach populations generally had higher genetic diversity than the stream populations, except for Knutson Beach and C Beach. Stream spawners varied in their genetic diversity. The A, C, and N4 stream populations had the lowest values for expected heterozygosity and allelic richness, with both measures being lowest in A Creek. Linkage-based N_e estimates ranged from 43 to infinitely large and were generally smaller for the stream populations than for the beaches populations (Table 1.4), but heterozygosity was not significantly correlated with N_e ($F = 0.31$, $P = 0.59$). Because the infinitely large population size could not be used for multivariate regression or calculating gene flow rates, these estimates were not used in subsequent analyses.

In terms of genetic differentiation, the sampled populations did not clearly group by ecotype based on the multidimensional scaling plot (Fig. 1.4; stress = 0.07, $r^2 = 0.99$), but there was some clustering by lake that was supported by AMOVA ($F_{CT} = 0.009$; $P < 0.001$). Nevertheless, a higher percentage of variation was partitioned among populations within lakes than among lakes ($F_{SC} = 0.012$; $P < 0.001$). The percentage of variation among ecotypes was negative and not significant ($F_{CT} = -0.008$, $P = 0.781$). There was no pattern of isolation by distance, either within the Wood River drainage ($P = 0.588$) or over all sampling sites ($P = 0.172$).

Genetic differentiation between beach and stream spawners varied by location (Table 1.5). For example, Elva and Knutson ecotypes were not differentiated ($F_{ST} < 0$; $G_{ST} = 0.005$), whereas A beach and stream spawners were highly differentiated ($F_{ST} = 0.0479$; $G_{ST} = 0.029$). In order from the most to the least differentiated, locations were ranked as follows: A, C, N4, Anvil/Hidden, Lynx, N6/Pick, Yako, Elva, Knutson. Differentiation between ecotypes as measured by F_{ST} was significant at A, C, N4, Anvil/Hidden, and Lynx (Table 1.5). Within ecotypes, differentiation between populations varied. F_{ST} values between beach spawner populations within the Wood River system were generally low ($F_{ST} = -0.0007$ to 0.011; Table S1) except for comparisons involving C Beach, which was differentiated from all other beach and stream populations with F_{ST} values of about 0.012 to 0.062. In contrast to the beach spawners, Wood River system stream spawners were sometimes differentiated from each other with F_{ST} values ranging from 0.001 to 0.069 (Table 1.S2).

Gene flow (in terms of dispersal rate ± standard deviation) could only be estimated for three ecotype pairs: A (beach ➔ stream 0.017±0.016, stream ➔ beach 0.078±0.035), C (beach ➔ stream 0.304±0.075, stream ➔ beach 0.130±0.072), and N4 (beach ➔ stream 0.190±0.059, stream ➔ beach 0.153±0.056). For all other beach-stream pairs, dispersal rates in both directions were approximately 0.5, indicating that BIMr had insufficient information to accurately estimate dispersal between those populations.

Effects of landscape and demographic factors on genetic differentiation

Based on weighted model averaging of AIC_C values (Table 1.6), stream depth was clearly the most informative predictor of genetic differentiation between ecotypes, followed by heterozygosity (mean of stream and beach populations at each site) and then by difference in male body length (based on predicted mean trait values from ANOVA). The confidence set of models included only the model with stream depth as a predictor, as no other candidate model had a weight that exceeded than 10% of the weight of the stream depth model. However, linear regressions suggested that both stream depth and population heterozygosity were significantly and negatively correlated with genetic differentiation between ecotypes within sites (Figs. 1.5 and 1.6; $F = 13.4$, $P = 0.008$, $r^2 = 0.75$ for stream depth; $F = 9.2$, $P = 0.02$, $r^2 = 0.47$ for heterozygosity). Stream depth and population heterozygosity were both included in a single regression model to test whether the pattern observed in stream depth was independent of the pattern observed in heterozygosity, and the regression showed that the coefficient for stream depth remained significant ($t = -3.1$; $P = 0.02$) even when heterozygosity ($t = -1.3$; $P = 0.25$) was included in the model.

Although not statistically significant, differentiation in male morphological traits generally showed a positive correlation with genetic differentiation between ecotypes (Figs. 1.7, 1. 8). Models including predictor variables based on male morphological traits always had higher weights than models with predictors based on female traits, and the morphological differences estimated using ANOVA (see Table 1.S3 for predicted trait means) usually ranked higher than the uncorrected differences (Table 1.6).

Linear regressions were also used to detect correlations between the landscape, fish morphology, and demographic variables, and results are presented in Table 1.7. Mean body depth and body length of stream males were highly correlated with stream depth at that location ($P < 0.05$), and heterozygosity was correlated with stream census size ($P = 0.05$; Table 6).

Simulations

Due to the fact that male body depth showed the largest and most consistent differentiation between ecotypes, we focus on results for that trait, although other traits showed similar but weaker patterns. Model simulations indicated that gene flow could have a strong and rapid homogenizing effect between phenotypes of beach and stream ecotypes, provided that the strength of stabilizing selection strength was weak or intermediate. For example, under a regime of intermediate stabilizing selection (correlation of selection $r_s = 0.5$), the difference in mean male body depth between the beach and stream populations was 35 mm when no dispersal occurred. When the bi-directional dispersal rate increased to 0.2, the mean difference between ecotypes decreased to 13 mm (Fig. 1.9). Thus, phenotypic homogenization appeared likely at the higher dispersal rates estimated by BIMr (0.13-0.30).

As stabilizing selection increased, however, phenotypic differentiation between ecotypes was maintained even as dispersal increased (Fig. 1.9). In addition, bi-directional dispersal rate had a greater effect on differences between ecotypes at lower dispersal rates (< 0.1), whereas stabilizing selection had a greater effect when dispersal rates were high (Fig. 1.9). Under each simulation scenario, mean trait differences equilibrated to a

common value after 100 years, with the rate of approach to equilibrium increasing with dispersal rate.

At low to moderate levels of stabilizing selection (r_s = 0.25-0.75; results averaged across dispersal rates), the relative reproductive success of immigrants to non-dispersing individuals was generally greater than 0.75 (Fig. 1.10). However, immigrant males had markedly lower reproductive success than the other non-immigrant males in the population when stabilizing selection was strong (Fig. 1.10). When stabilizing selection was held constant, increasing dispersal increased relative reproductive success of immigrants, as both immigrant and non-immigrant individuals became more phenotypically similar. Under our simulation conditions, we found no stabilizing selection threshold at which dispersers completely lacked reproductive success, for either sex. In other words, adaptive divergence never eliminated gene flow between the populations.

Discussion

The goal of this project was to better understand how interactions between gene flow and local adaptation may determine genetic and phenotypic divergence between sockeye salmon populations. In the first part of this study, we quantified genetic and phenotypic differentiation between adjacent beach and stream ecotype populations and determined the environmental and demographic factors that may have influenced the magnitude of differentiation. Levels of genetic differentiation between ecotypes varied, with F_{ST} values ranging from -0.001 to 0.048. Weighted model averaging with AIC_C values indicated that stream depth was the most important factor contributing to that

differentiation, followed by heterozygosity. Genetic differentiation was also positively correlated (albeit not significantly) with phenotypic differentiation between ecotypes, especially with regard to male morphological traits. These results suggested that gene flow might be higher at sites with deeper streams, resulting in reduced phenotypic divergence, or alternatively, phenotypic divergence might reduce gene flow between ecotypes at sites with shallow streams. For the second part of this study, we used a simulation model to determine how gene flow and adaptive divergence may interact to influence phenotypic differentiation between ecotype populations. The model demonstrated that gene flow can rapidly homogenize phenotypes between populations, but that strong stabilizing selection within populations can help maintain phenotypic divergence even when gene flow occurs.

The most plausible explanation for the shallowest streams being the most differentiated from their neighboring beach populations was that stream depth affected levels of dispersal and gene flow between habitats, potentially in both directions. Beach to stream dispersal may be limited at sites with shallower streams because large beach spawners, especially the deep-bodied males, are at higher risk for predation and stranding (Carlson & Quinn 2007; Quinn & Buck 2001). Moreover, stream to beach dispersal may be limited at these sites due to sexual selection. Fish from shallower streams tend to be smaller than those from deeper streams (demonstrated here and in Quinn *et al.* 2001b), and females typically prefer mates as large as or larger than themselves, presumably because larger body size indicates higher fitness (Foote 1988, 1989). Small-bodied stream immigrants may therefore have reduced mating success in beach habitats. Female

body sizes are more similar between ecotypes, but divergent selection could still occur. For instance, larger females are also preferentially targeted by bears in shallow streams (Quinn & Buck 2001), and small stream females may have more difficulty constructing and guarding redds in beach habitat. Nevertheless, sex-specific differences in natural and sexual selection could use additional study.

Heterozygosity (mean of the stream and beach populations at each site) also appeared to contribute to genetic differentiation, with ecotypes generally being more differentiated at sites with lower heterozygosity. Low heterozygosity is associated with low effective population size and potentially suggests that genetic drift will affect the population. However, factors other than genetic drift may also have influenced differentiation patterns. For example, population bottlenecks may have increased genetic divergence of the N4 Creek population, which has an intermittent presence of salmon (Moore & Schindler 2008). At other locations, ecotype populations may be only recently diverged. In cases of recent divergence, populations may reach an equilibrium in phenotypic differentiation before reaching an equilibrium in genetic differentiation, as hundreds of generations may be required to achieve migration-drift equilibrium, especially if effective population sizes are large (Whitlock & McCauley 1999). Even if factors such as bottlenecks and recent divergence were present, however, the observed relationship between genetic differentiation and heterozygosity does suggests that genetic drift affected genetic divergence patterns in these systems.

Although not statistically significant, there were also positive correlations between genetic and morphological differentiation between ecotypes at each site (Figs.

1.7 and 1.8). The lack of significance likely resulted from lack of power, as these regressions were based on only nine population pairs. In addition, temporal variation in body sizes within each population (e.g. Pyper & Peterman 1999) may have compromised the signal of morphological differentiation between ecotypes, despite our attempts to correct for different sampling efforts using ANOVA. Nevertheless, the positive correlation between genetic and morphological differentiation may be indicative of reduced gene flow between phenotypically divergent populations, higher gene flow between phenotypically similar populations, or both. For example, the small salmon occurring in A and C creeks may have difficulty spawning at beach sites because they are less competitive in terms of sexual selection, whereas large stream spawners from Knutson Creek would not have this constraint if they attempted to spawn at Knutson Beach.

Thus, the empirical results indicated that divergent selection might restrict gene flow between ecotypes, but gene flow in turn may have reduced phenotypic divergence at some of the study sites. Unfortunately, we were unable to distinguish between these hypotheses by empirically estimating dispersal rates between ecotype populations. BIMr estimated migration rates for only the three sites where pairwise F_{ST} between ecotypes was greater than 0.01, and the estimated rates varied from 0.02 to 0.2. In addition, there was no consistent pattern of higher gene flow from stream to beach or vice versa that would suggest that migrants from one habitat were more reproductively successful. Despite the lack of precision, BIMr indicated that gene flow may occur even at the sites

with high genetic and phenotypic differentiation, and the program also provided migration estimates for use in the simulation model.

Interestingly, the model results supported the idea that strong divergent selection can maintain phenotypic differences between ecotypes despite gene flow. Although gene flow always reduced local adaptation within each population, strong stabilizing selection maintained substantial phenotypic differentiation between ecotypes, especially at high dispersal rates (Fig. 1.9). Stabilizing selection favored phenotypes close to the local population optimum, but even the highest level of stabilizing selection in our model was insufficient to completely eliminate gene flow between ecotypes (Fig. 1.10). This result was partly due to the model structure, which did not substantially lower the mating success of phenotypically-distinct immigrants. First, the likelihood of dispersal was random with respect to phenotype. Second, immigrant females always mated successfully, and mating success for immigrant males was determined simply by body length, with larger individuals having increased success. Perhaps more importantly however, there was sufficient phenotypic variation within offspring produced by immigrant parents that some always survived stabilizing selection, suggesting that environmentally-induced variation (phenotypic plasticity) may facilitate adaptive evolution (Ghalambor *et al.* 2007), a result that warrants further investigation.

Nonrandom dispersal is a second mechanism that can maintain phenotypic differences despite gene flow. If the likelihood of dispersal is greater for individuals that are more phenotypically similar to the fish in the recipient population, the homogenizing effects of gene flow on phenotypes would be mitigated, and gene flow might even

contribute to divergence (Garant *et al.* 2005). In fact, we previously found that, at A and C, putative male dispersers between beach and stream habitats had body depths resembling those of males in the habitats to which they immigrated (Lin *et al.* 2008a). Dispersers may therefore move into habitats where their phenotypes are adaptive, or they may be forced to disperse because their phenotypes are maladaptive in their native habitats. As for selection against immigrants, crossing of distinct salmonid populations can have varied effects on fitness (McClelland & Naish 2007), including outbreeding depression (e.g. Gilk *et al.* 2004). Since beach and stream sockeye salmon ecotypes show considerable phenotypical differences, as shown by this study, negative effects of outbreeding are quite possible. Evidence for nonrandom dispersal is increasing (Garant *et al.* 2007), and our results support this trend.

Given the empirical data and the simulation results, we strongly suspect that selection maintains phenotypic differentiation between sockeye salmon ecotypes at some of the study sites. This was apparent for the Hidden Lake Creek/Anvil Bay Beach population pair, as the ecotypes were phenotypically distinct despite the high potential dispersal rate populations ($m > 0.5$) suggested by BIMr. However, strong selection may also have increased phenotypic differentiation between ecotypes at other sites such as C, where BIMr suggested gene flow despite significant genetic differentiation.

We focused primarily on genetic differentiation between ecotypes at each site based on our research question, but dispersal between more distant populations, population census sizes, and intra-seasonal genetic variation within populations may also affect genetic structure. Gene flow among populations within lakes may be common, as

we observed genetic clustering of beach ecotypes by lake (Fig. 1.3), and genetic differentiation between nursery lakes has been observed previously in sockeye salmon (Wood 1995). Population census sizes would potentially affect the absolute number of dispersers between ecotypes at each site, which could affect phenotypic differentiation patterns. For example, the Elva Beach population is much larger than the Elva Creek population, and thus a 5% bi-directional dispersal rate between these ecotypes would cause the proportion of strays (and hence their genetic influence) to be substantially greater in the stream population. Nevertheless, the simulations showed that the interaction between selection and gene flow between populations was more important in determining phenotypic differentiation between ecotypes than gene flow itself, and variation in gene flow from other populations should not alter the study conclusions. Another important observation is that intra-seasonal genetic variation in our system is minimal, as a separate analysis by the Alaska Department of Fish and Game found that Knutson beach spawners sampled nearly two months apart were not genetically distinct (T. Dann, pers. comm.). Moreover, collecting beach and stream samples during a period of temporal overlap limited any confounding effects of temporal segregation on genetic differentiation.

Genetic analysis of samples collected over multiple years would have provided insight as to whether the observed correlations between genetic differentiation and both stream depth and heterozygosity are consistent over time. However, temporal analysis of samples was not considered critical for accomplishing the goals of this study, especially since previous work in sockeye salmon indicates that patterns of genetic differentiation

among populations often persist over the short term (Fillatre *et al.* 2003). There was no reason to suspect that our study populations would differ in this respect, and indeed, data collected at A and C for a previous study showed that F_{ST} values between ecotypes at each site remained comparable over three consecutive years (Lin *et al.* 2008a).

By combining empirical data with simulation modeling, we showed how local adaptation and gene flow may interact in sockeye salmon. Theory holds that gene flow may counter selection and constrain population divergence and local adaptation (Slatkin 1987), with the effects having major implications for population fitness (Lenormand 2002). For instance, gene flow apparently lowered survival in one great tit population, because the source and recipient populations experienced different selection regimes and were adapted for different environmental conditions (Garant *et al.* 2005; Postma & van Noordwijk 2005). In sockeye salmon, gene flow will homogenize phenotypes and potentially lead to population maladaptation as well. However, our results suggested that strong selective pressures can maintain phenotypic differences between ecotypes even when some gene flow occurs. If selection against immigrants increases over time, adaptive differences may eventually accumulate to a point where they limit gene flow (Quinn *et al.* 2000; Schluter 1996).

In conclusion, the results offered some useful insights about the ecology and evolution of beach and stream sockeye ecotypes. Environment appears to affect genetic differentiation between ecotypes, via natural and/or sexual selection against phenotypically distinct immigrants. This natural variation in divergence will potentially contribute to system biocomplexity and resilience. In addition, gene flow rates and

genetic differentiation between any particular pair of populations may change over time as environmental shifts occur. For example, if lake level is high in a particular year, even the relatively shallow streams will have increased water depth at their mouths, potentially providing easier access for larger-bodied individuals (Carlson & Quinn 2007) and increased gene flow between populations. The role of environmental variability, both spatial and temporal, is therefore worth considering in regards to the maintenance of intraspecific diversity in sockeye salmon.

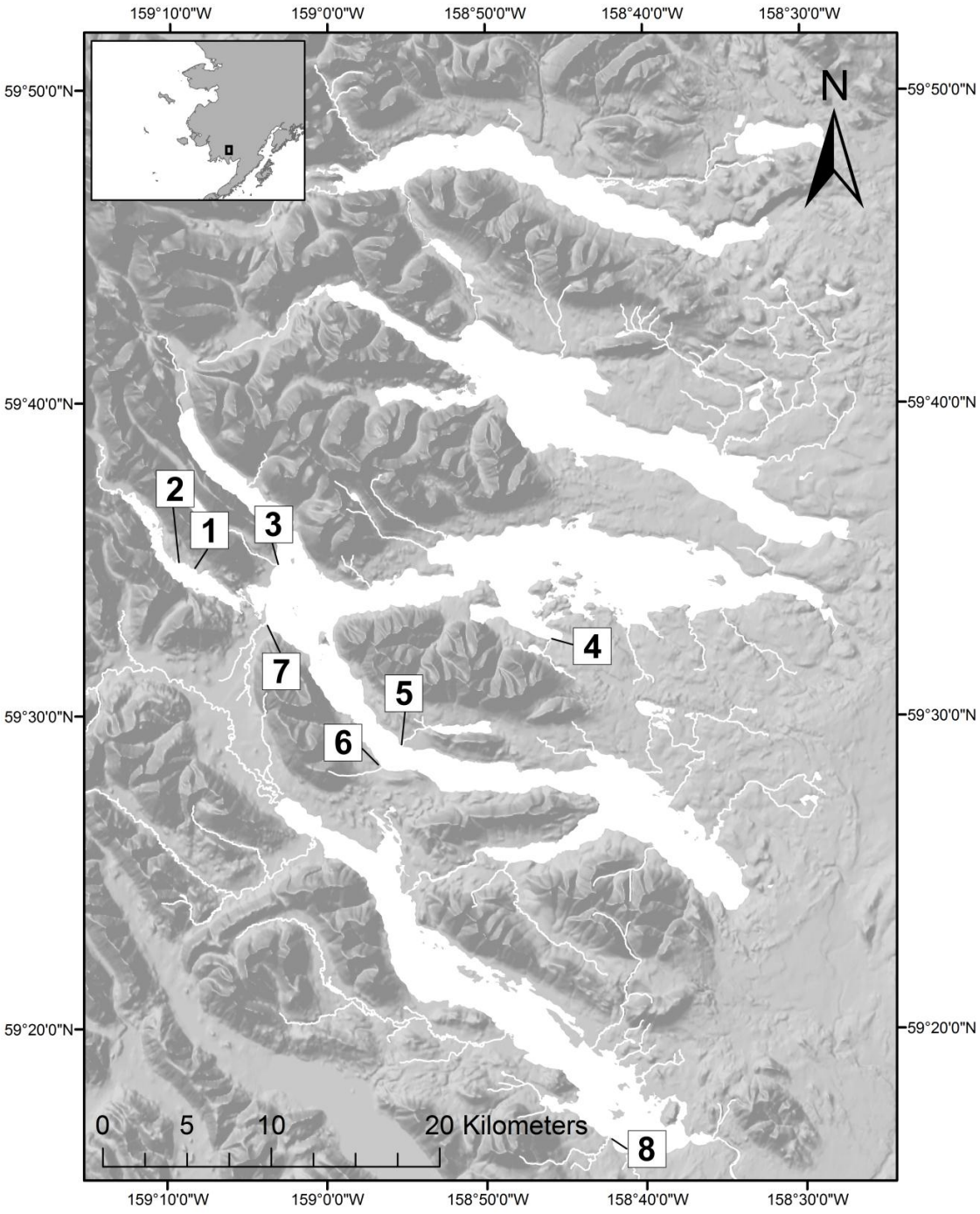


Figure 1.1. Map of the study site locations in the Wood River Lakes system in southwestern Alaska. The sites are listed by number in Table 1.1.

Figure 1.2. Map of the study site location in the Iliamna Lake system in southwestern Alaska. The site is listed by number in Table 1.1.

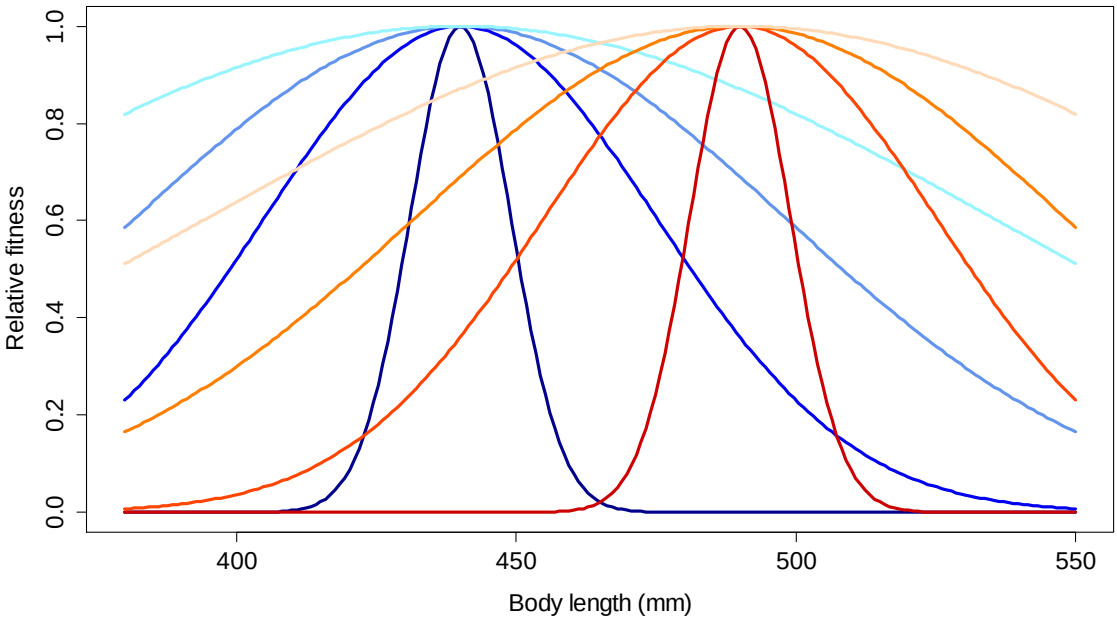


Figure 1.3. Relationship between body length (mm) and relative fitness (varying from 0 to 1), assuming two optima for body length: 440 mm and 490 mm. The blue lines represent fitness curves for the 440 mm optimum, and the orange lines represent fitness curves for the 490 mm optimum. The fitness curves for each optimum differ in the level of stabilizing selection assumed (r_s = 0.25, 0.50, 0.75, or 1.0); the lighter the color of the fitness curve, the lower the level of stabilizing selection assumed.

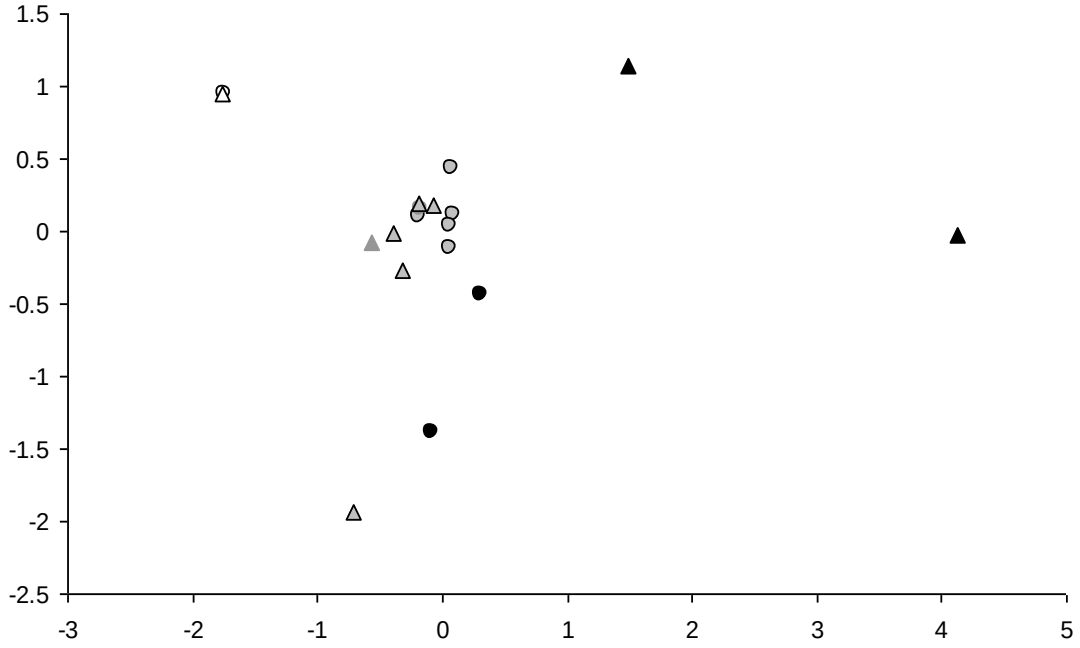


Figure 1.4. Multidimensional scaling plot of F_{ST} values (Weir & Cockerham 1984). Different symbol colors represent different lakes (Aleknagik=grey, Nerka=grey outlined in black, Little Togiak=black, Iliamna=white). Circles represent beach-spawning populations, and triangles represent stream-spawning populations. The stress value is 0.07, and $r^2 = 0.99$.

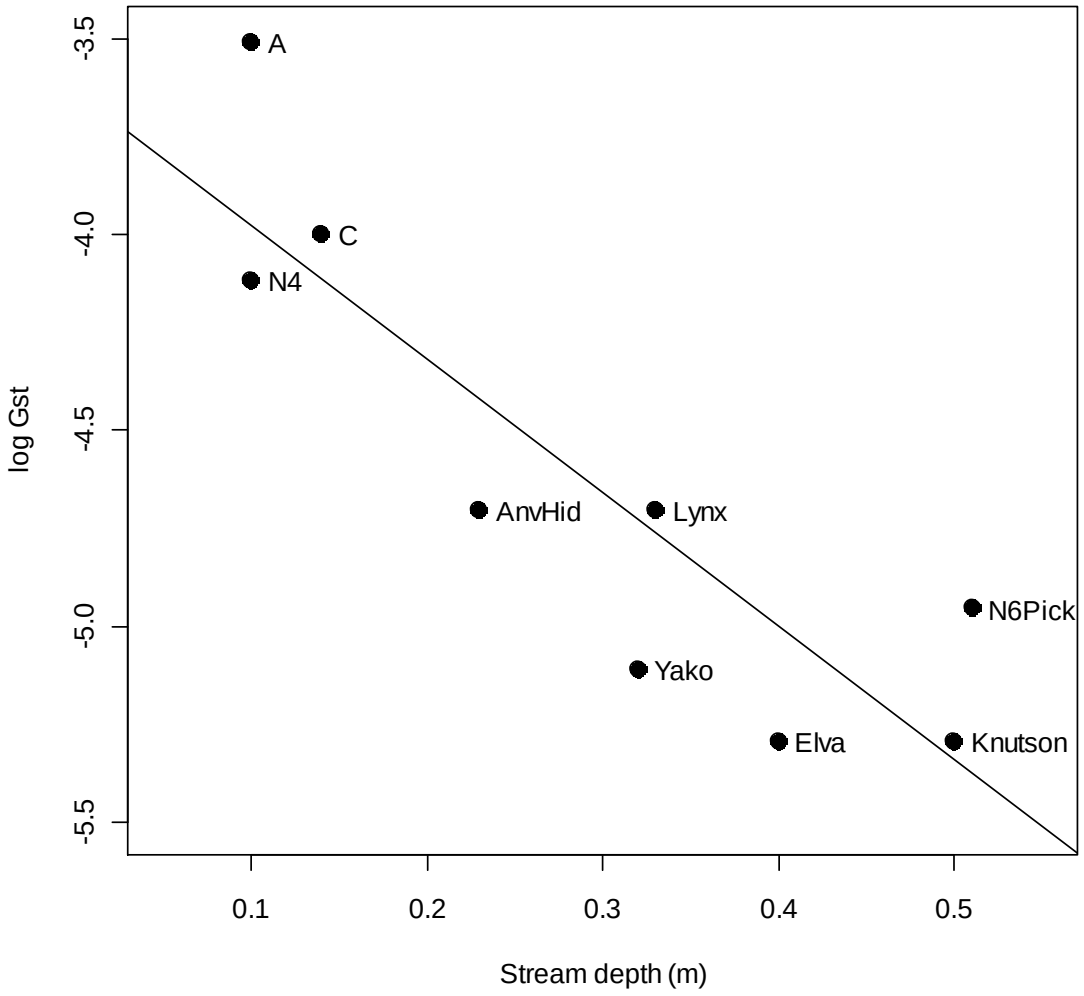


Figure 1.5. Mean stream depth versus pairwise G_{ST} between ecotypes at each site (logit-transformed). Each point represents data from a specific beach-stream population pair. The line is the fitted linear regression model ($r^2 = 0.75$, $P = 0.008$).

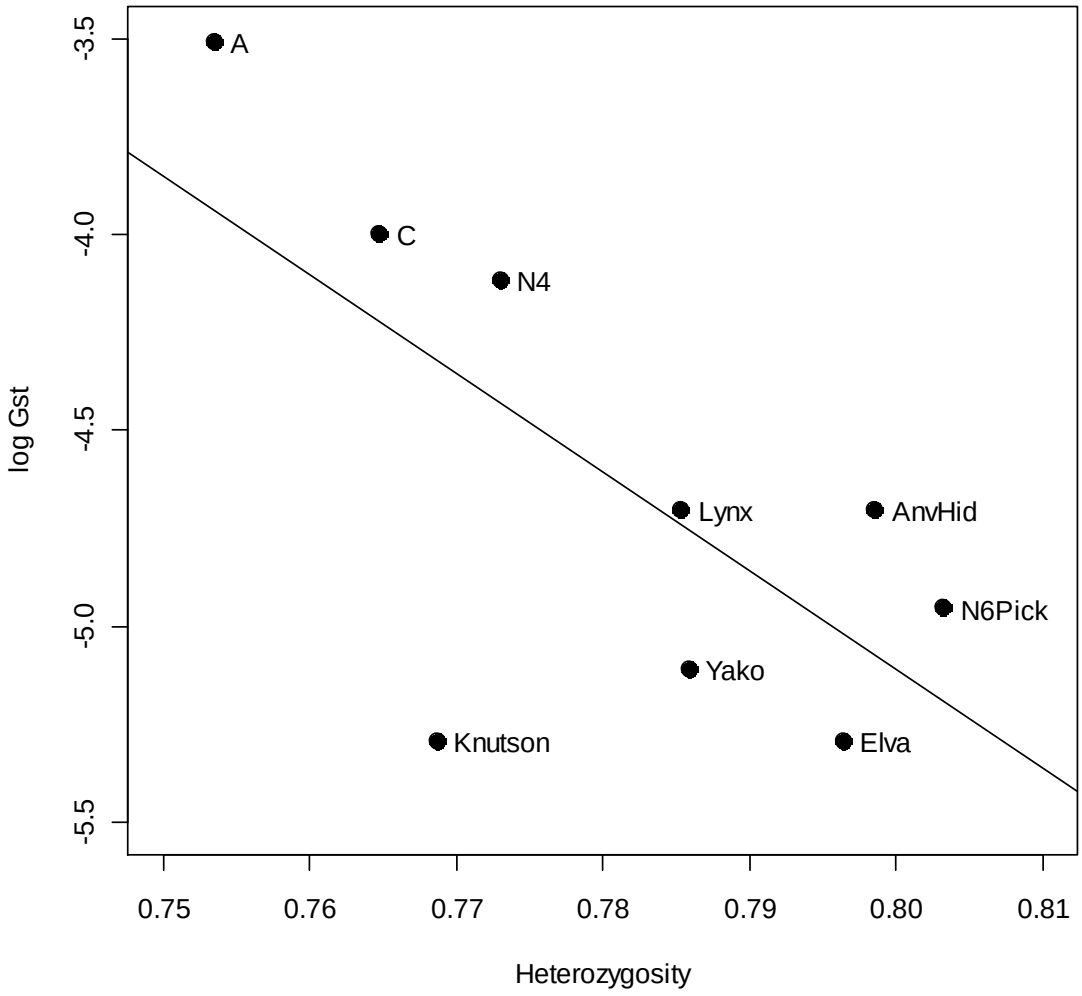


Figure 1.6. Mean expected heterozygosity for the beach and stream populations at each site versus pairwise G_{ST} between ecotypes at each site (logit-transformed). Each point represents data from a specific beach-stream population pair. The line is the fitted linear regression model ($r^2 = 0.47$, $P = 0.02$).

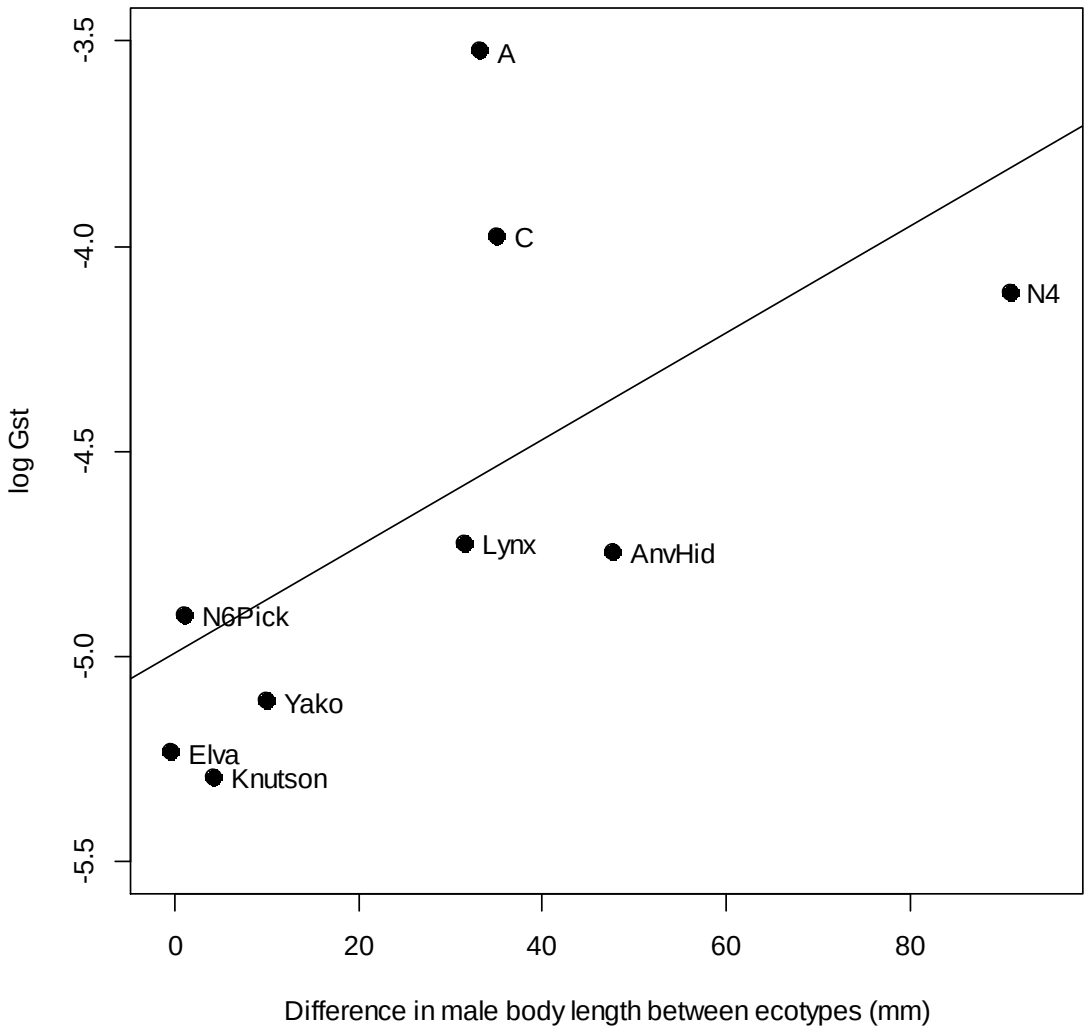


Figure 1.7. Difference in mean male body length versus pairwise G_{ST} (logit-transformed) between ecotypes at each site. The difference in body length is based on predicted mean trait values from ANOVA. Each point represents data from a specific beach-stream population pair. The line is the fitted linear regression model ($r^2 = 0.27$, $P = 0.15$).

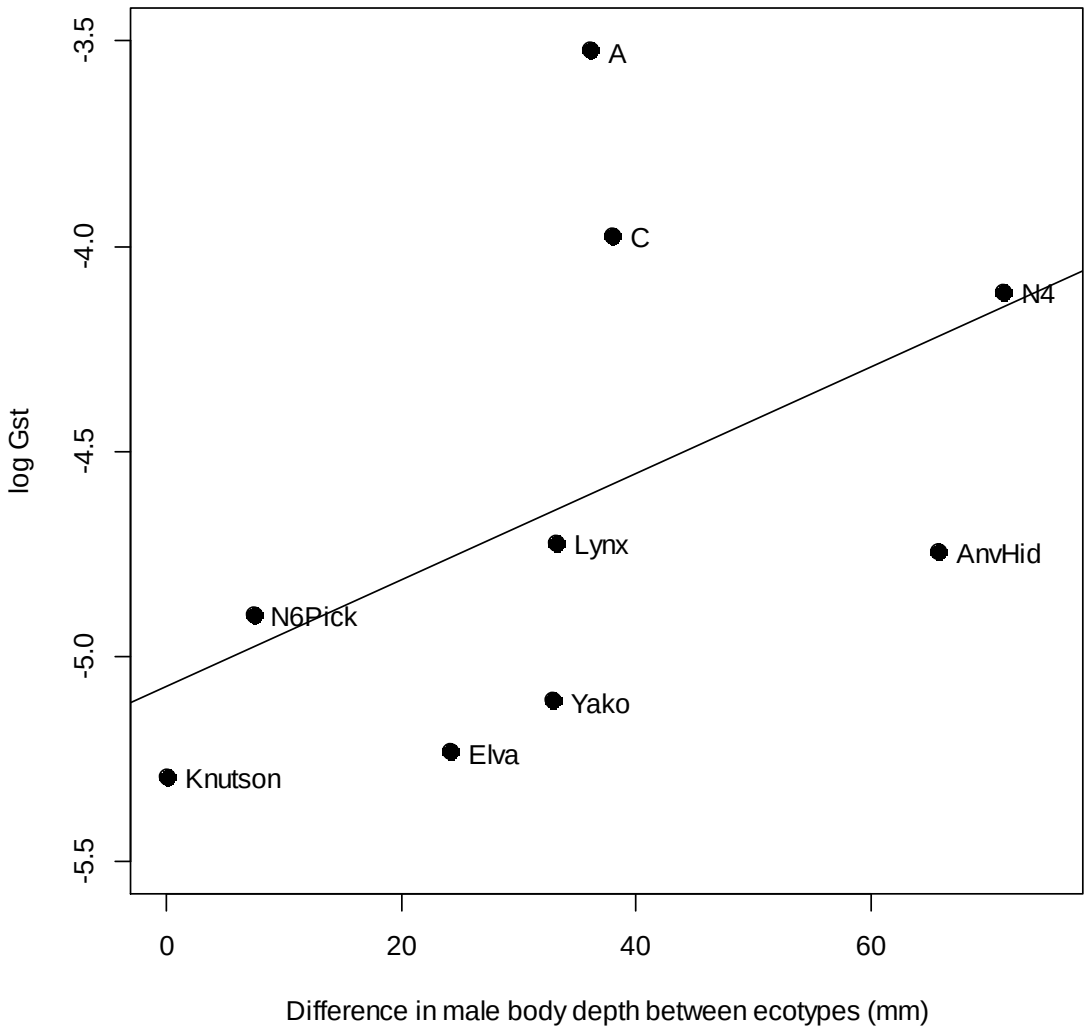


Figure 1.8. Difference in mean male body depth versus pairwise G_{ST} (logit-transformed) between ecotypes at each site. The difference in body depth is based on predicted mean trait values from ANOVA. Each point represents data from a specific beach-stream population pair. The line is the fitted linear regression model ($r^2 = 0.23$, $P = 0.20$).

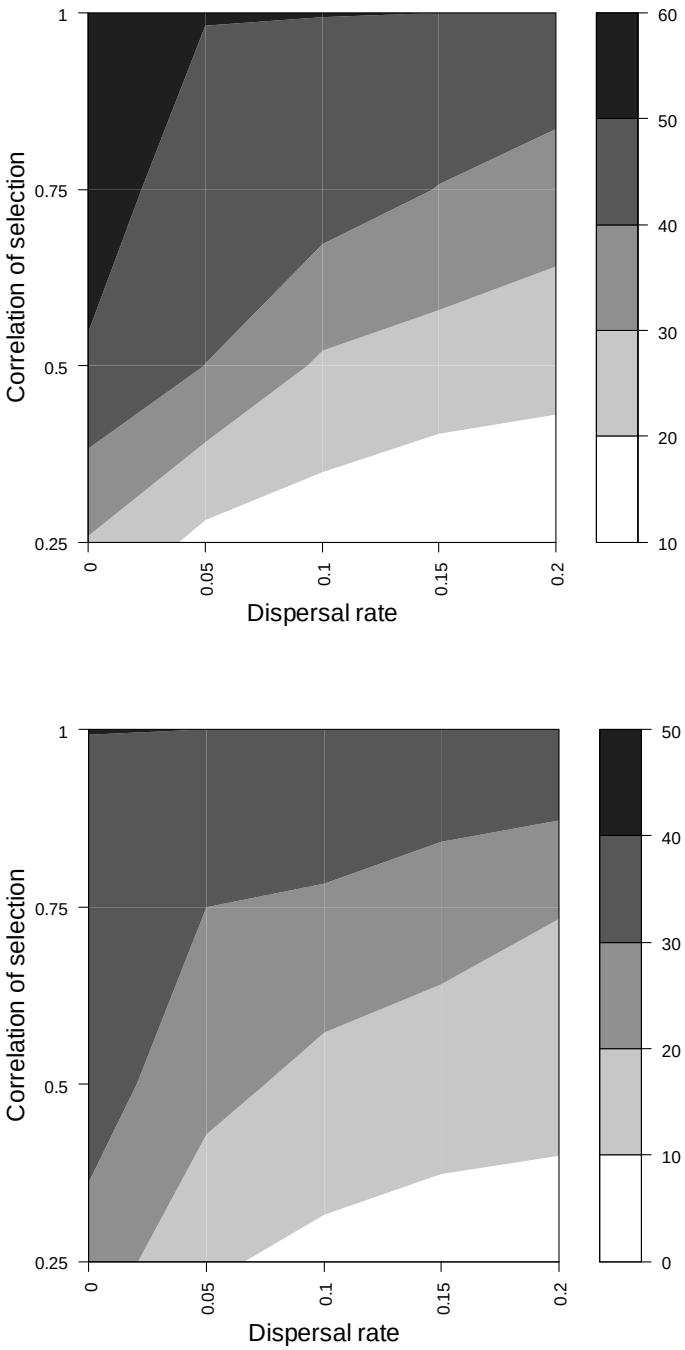


Figure 1.9. Contour plots of mean difference in mean male body length (top) and body depth (bottom) between the simulated local beach and stream populations in mm, considering different combinations of stabilizing selection and dispersal rate between the populations. The different shades represent different levels of mean phenotypic differences, with darker colors associated with larger differences.

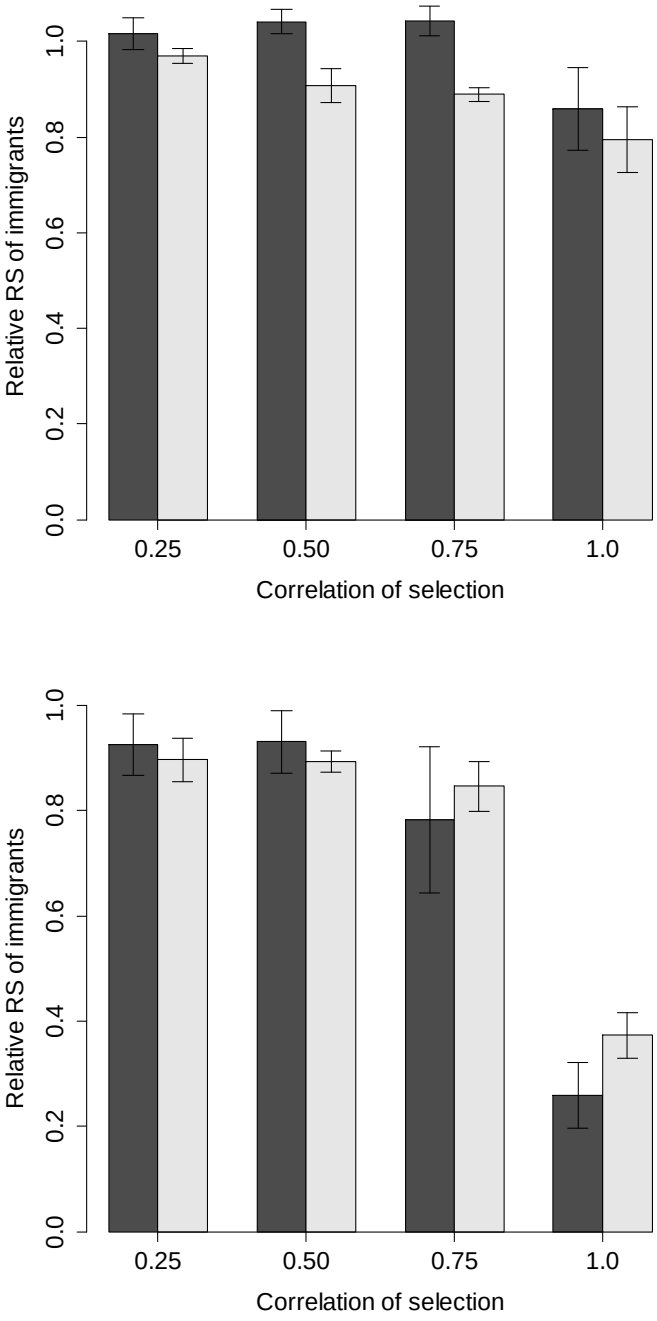


Figure 1.10. Relative reproductive success of immigrants to non-dispersing individuals after 100 years, under different stabilizing selection regimes and averaged across dispersal rates. Data from the simulated stream population is dark grey, and data from the simulated beach population is light grey. Female data are on top, and male data are on the bottom. Error bars represent the standard deviation.

Table 1.1. Habitat and population data for the study streams. Depth refers to wetted stream depth, length refers wetted stream length accessible to spawning fish, and width refers to wetted stream width. Stream population size estimates (standard deviation in parentheses) were estimated from stream survey data. Sites where the stream population was generally larger than the beach population are marked with a "Y" in the "Stream population larger" column. Distance between ecotypes is the water distance between the populations. Beach population sizes were estimated visually.

Site	Stream	Depth (m)	Length (km)	Width (m)	Population size and SD	Stream population larger	Distance between ecotypes (m)	Beach population size
1	A Creek	0.10	0.37	1.30	345 (175)	Y	10	50-100
2	C Creek	0.14	0.44	1.60	292 (144)	Y	10	50-100
3	Elva Creek	0.40	0.50	6.72	200 (73)	N	41	500-2000
4	Hidden Lake Creek	0.23	1.60	4.21	2263 (4438)	N	760	5000-50000
5	Lynx Creek	0.33	3.00	6.90	2171 (6765)	Y	83	500 - 2000
6	N4 Creek	0.10	0.50	4.10	354 (0)	N	64	5000-50000
7	Pick Creek	0.51	2.30	6.45	11390 (5078)	Y	3150	5000-50000
8	Yako Creek	0.32	2.80	3.30	1651 (4517)	Y	110	500-1000
9	Knutson Creek	0.50	19.00	12.20	590 (1742)	N	10	1000-10000

Table 1.2. Summary of morphological data for the sampled sockeye salmon. Mean values for each trait are in mm and followed by the standard deviation in parentheses.

	A	C	Elva	Anv/Hid	Lynx	N4	N6/Pick	Yako	Knutson
Female length									
Beach	436 (32)	433 (33)	427 (28)	447 (39)	447 (38)	435 (32)	414 (22)	418 (27)	441 (33)
Stream	422 (28)	420 (26)	419 (28)	425 (33)	431 (30)	422 (21)	435 (36)	437 (34)	438 (32)
Male length									
Beach	470 (39)	464 (37)	441 (42)	485 (38)	484 (38)	473 (38)	456 (40)	446 (54)	458 (38)
Stream	430 (34)	431 (33)	453 (36)	441 (46)	421 (74)	425 (41)	464 (43)	450 (46)	459 (31)
Female depth									
Beach	113 (15)	115 (12)	120 (17)	131 (17)	131 (14)	124 (13)	116 (10)	116 (13)	130 (11)
Stream	105 (10)	107 (10)	96 (9)	108 (10)	119 (14)	99 (7)	113 (14)	116 (14)	120 (10)
Male depth									
Beach	167 (27)	169 (26)	174 (23)	187 (24)	198 (22)	181 (28)	164 (22)	164 (33)	163 (22)
Stream	125 (15)	131 (16)	150 (26)	124 (13)	164 (21)	127 (16)	155 (21)	135 (19)	172 (16)
Female standardized depth									
Beach	117 (13)	120 (8)	131 (13)	132 (7)	132 (8)	129 (7)	129 (7)	127 (9)	128 (7)
Stream	131 (13)	116 (8)	106 (9)	118 (7)	121 (10)	104 (7)	120 (9)	121 (10)	120 (10)
Male standardized depth									
Beach	155 (18)	160 (15)	179 (10)	170 (13)	181 (10)	169 (18)	161 (13)	165 (14)	153 (12)
Stream	133 (10)	139 (11)	151 (10)	133 (9)	156 (12)	132 (14)	153 (9)	136 (9)	167 (9)

Table 1.3. Parameter values used in the individual-based simulation model to determine phenotypic traits of the fish. These values also represent the optimum phenotypes within each population. The global and local beach populations used the same parameter values.

Parameter	Stream female	Stream male	Beach female	Beach male
Mean age	4.5	4.5	5.2	5.2
Std dev age	0.4	0.6	0.6	0.6
Mean length (mm)	430	440	460	490
Std dev length (mm)	30	35	35	35
Mean depth (mm)	115	140	135	180
Std dev depth (mm)	15	20	15	20

Table 1.4. Summary genetic statistics for each sampled population. *N* is the mean number of individuals which were successfully genotyped, N_a is the mean number of alleles, H_o is observed heterozygosity, H_e is expected heterozygosity, *HWE* is probability of being out of Hardy-Weinberg equilibrium due to heterozygote deficiency (Guo & Thompson 1992), F_{IS} is the inbreeding coefficient (Weir & Cockerham 1984), *AR* is allelic richness, and N_e is effective population size estimated by LDNE. The N_e estimates are followed by the 95% confidence interval in parentheses.

	N	N_a	H_o	H_e	*HWE*	F_{IS}	*AR*	N_e
A Beach	47	13.5	0.82	0.80	0.33	0.00	12.8	1928 (359, infinite)
A Creek	47	8.4	0.72	0.70	0.61	-0.02	8.2	84 (62, 124)
C Beach	48	12.2	0.76	0.77	0.12	0.02	11.4	43 (37, 50)
C Creek	48	10.7	0.78	0.76	0.15	-0.02	10	65 (52, 85)
Elva Beach	46	13	0.80	0.80	0.01	0.02	12.5	484 (217, infinite)
Elva Creek	45	13.5	0.79	0.80	0.14	0.01	12.9	109 (82, 156)
Anvil Bay Beach	46	13.5	0.79	0.79	0.13	0.00	12.9	23500 (390, infinite)
Hidden Lake Creek	46	13.3	0.78	0.81	0.00	0.06	12.8	1123 (310, infinite)
Lynx Beach	47	13.4	0.78	0.78	0.46	0.00	12.9	168 (119, 273)
Lynx Creek	47	13.8	0.80	0.79	0.52	-0.01	13.1	556 (242, infinite)
N4 Beach	48	13.3	0.81	0.80	0.26	0.00	12.6	Infinite
N4 Creek	48	11.1	0.73	0.75	0.02	0.04	10.5	76 (60, 100)
N6 Beach	46	13.2	0.80	0.79	0.44	0.00	12.6	128 (94, 194)
Pick Creek	47	13.5	0.80	0.81	0.10	0.02	12.9	861 (289, infinite)
Yako Beach	48	13.3	0.80	0.79	0.29	-0.01	12.6	1350 (328, infinite)
Yako Creek	48	13.9	0.78	0.78	0.03	0.01	13.1	247 (156, 546)
Knutson Beach	46	13.8	0.73	0.77	0.00	0.04	13.2	990 (293, infinite)
Knutson Creek	45	14.3	0.77	0.77	0.00	0.00	13.7	381 (198, 2949)

Table 1.5. Measures of genetic differentiation between beach and stream ecotypes at the sampled sites. F_{ST} is Weir and Cockerham's theta (1984) and G_{ST} is Nei's G_{ST} (1973).

	F_{ST}	G_{ST}
A	0.048	0.029
C	0.025	0.018
Elva	0.000	0.005
AnvHid	0.007	0.009
Lynx	0.006	0.009
N4	0.022	0.016
N6Pick	0.004	0.007
Yako	0.002	0.006
Knutson	0.000	0.005

Table 1.6. Comparison of linear regression models with genetic differentiation between ecotypes as the dependent variable and other factors as the model predictors, with models ordered from low to high AIC_C value. Heterozygosity = mean expected heterozygosity of the beach and stream populations within a site. The morphological predictors (length = body length, abs depth = absolute body depth, std depth = standardized body depth) represent the difference between mean trait values between ecotypes within a site, where the difference was calculated as the difference in absolute mean trait values between ecotypes (suffix = 1) or as the difference in mean trait values between ecotypes predicted by ANOVA (suffix = 2). *K* is the number of parameters in the model, AIC*c* is the AIC*c* value, w_i is the Akaike weight (normalized relative likelihood of the model), Coef. is the model coefficient, and *P* val. is the *p*-value for the coefficient.

Model predictors	*K*	AICc	w_i	r^2	Coef.	*P* val.
Stream depth	2	14.3	0.89	0.74	-3.32	0.00
Heterozygosity	2	20.9	0.03	0.47	-24.74	0.04
Male length 1	2	21.8	0.02	0.41	0.01	0.06
Male length 2	2	22.4	0.02	0.37	0.01	0.08
Male abs depth 1	2	23.0	0.01	0.33	0.02	0.11
Male abs depth 2	2	24.0	0.01	0.25	0.01	0.17
Female length	2	24.5	0.01	0.20	0.02	0.22
Male std depth 1	2	25.6	0.00	0.11	0.01	0.39
Female length 1	2	25.7	0.00	0.09	0.01	0.43
Male std depth 2	2	26.1	0.00	0.05	0.01	0.55
Female std depth 1	2	26.1	0.00	0.05	-0.02	0.55
Female std depth 2	2	26.3	0.00	0.03	-0.01	0.63
Female abs depth 1	2	26.6	0.00	0.00	0.00	0.97
Female abs depth 2	2	26.6	0.00	0.00	0.00	0.99

Table 1.7. Results of linear regression tests for correlations between landscape, fish morphology, and demographic variables. FD = female body depth, FL = female body length, MD = male body depth, ML = male body length, and *N* refers to the stream census population size. Correlations with $P < 0.05$ were considered significant and are marked with an asterisk

Variable 1	Variable 2	r^2	*F*	*P*
Stream depth	Beach FD	0.11	0.89	0.38
Stream depth	Beach FL	0.00	0.00	0.97
Stream depth	Beach MD	0.00	0.01	0.93
Stream depth	Beach ML	0.05	0.40	0.55
Stream depth	Stream FD	0.26	2.45	0.16
Stream depth	Stream FL	0.40	4.68	0.07
Stream depth	Stream MD	0.76	21.8	0.00*
Stream depth	Stream ML	0.76	22.3	0.00*
Stream depth	Heterozygosity	0.33	3.37	0.11
Stream depth	*N*	0.32	3.31	0.11
Heterozygosity	Beach FD	0.01	0.08	0.78
Heterozygosity	Beach FL	0.13	1.07	0.34
Heterozygosity	Beach MD	0.01	0.05	0.83
Heterozygosity	Beach ML	0.06	0.44	0.53
Heterozygosity	Stream FD	0.00	0.02	0.90
Heterozygosity	Stream FL	0.03	0.25	0.63
Heterozygosity	Stream MD	0.06	0.43	0.53
Heterozygosity	Stream ML	0.19	1.61	0.25
Heterozygosity	*N*	0.44	5.47	0.05

Table 1.S1. Summary genetic information for each locus within each population. *N* is the mean number of individuals which were successfully genotyped, H_o is observed heterozygosity, H_e is expected heterozygosity, *HWE* is probability of being out of Hardy-Weinberg equilibrium due to heterozygote deficiency (Guo & Thompson 1992), and F_{IS} is the inbreeding coefficient (Weir & Cockerham 1984).

Sample	Locus	*N*	*H*o	*H*e	*HWE*	F_{IS}
A Beach	One100	47	0.89	0.91	0.23	0.03
	One102	47	0.87	0.82	0.36	-0.05
	One103	47	1.00	0.95	1.00	-0.04
	One108	47	0.87	0.87	0.38	0.01
	One109	47	0.81	0.82	0.21	0.02
	One110c	47	0.96	0.91	0.58	-0.04
	One112	47	0.85	0.87	0.67	0.03
	One114	47	0.85	0.90	0.17	0.06
	Ots3	47	0.72	0.65	0.88	-0.10
	OtsG68	47	0.72	0.71	0.06	-0.01
	Ots103	47	0.98	0.89	0.98	-0.09
	Ots107	47	0.30	0.36	0.02	0.18
A Creek	One100	45	0.71	0.77	0.01	0.08
	One102	47	0.83	0.80	0.86	-0.03
	One103	47	0.94	0.91	0.73	-0.02
	One108	47	0.87	0.84	0.61	-0.03
	One109	47	0.70	0.68	0.51	-0.03
	One110c	47	0.83	0.75	0.81	-0.10
	One112	47	0.66	0.80	0.06	0.19
	One114	47	0.94	0.88	0.87	-0.06
	Ots3	47	0.51	0.48	0.76	-0.05
	OtsG68	47	0.57	0.51	0.88	-0.12
	Ots103	47	0.81	0.81	0.36	0.02
	Ots107	47	0.26	0.22	1.00	-0.14
C Beach	One100	48	0.71	0.87	0.01	0.20
	One102	48	0.81	0.76	0.78	-0.06
	One103	48	0.85	0.91	0.22	0.08
	One108	48	0.65	0.84	0.01	0.24
	One109	48	0.85	0.85	0.53	0.00
	One110c	48	0.88	0.86	0.45	-0.01
	One112	48	0.92	0.86	0.67	-0.05

Table 1.S1, continued.

	One114	48	0.88	0.89	0.52	0.02
	Ots3	48	0.56	0.50	0.84	-0.11
	OtsG68	48	0.69	0.67	0.49	-0.02
	Ots103	48	0.90	0.86	0.90	-0.03
	Ots107	48	0.38	0.38	0.47	0.03
C Creek	One100	47	0.74	0.85	0.01	0.14
	One102	48	0.83	0.83	0.61	0.01
	One103	48	0.94	0.93	0.14	0.00
	One108	48	0.96	0.88	0.81	-0.08
	One109	48	0.79	0.81	0.40	0.04
	One110c	48	0.92	0.82	0.96	-0.10
	One112	48	0.83	0.79	0.83	-0.05
	One114	48	0.88	0.86	0.54	-0.01
	Ots3	48	0.46	0.45	0.16	-0.02
	OtsG68	48	0.73	0.68	0.07	-0.07
	Ots103	48	0.81	0.81	0.34	0.01
	Ots107	48	0.46	0.39	0.93	-0.15
Elva Beach	One100	46	0.89	0.91	0.34	0.04
	One102	47	0.81	0.84	0.00	0.04
	One103	44	0.98	0.94	0.80	-0.03
	One108	47	0.94	0.89	0.77	-0.04
	One109	48	0.85	0.86	0.42	0.02
	One110c	47	0.91	0.91	0.53	0.00
	One112	46	0.89	0.86	0.46	-0.03
	One114	43	1.00	0.90	1.00	-0.10
	Ots3	48	0.58	0.57	0.06	-0.01
	OtsG68	47	0.62	0.65	0.12	0.06
	Ots103	46	0.83	0.89	0.00	0.09
	Ots107	45	0.27	0.34	0.06	0.21
Elva Creek	One100	45	0.89	0.92	0.24	0.05
	One102	46	0.89	0.86	0.62	-0.03
	One103	47	0.96	0.94	0.50	-0.01
	One108	45	0.87	0.86	0.24	0.00
	One109	46	0.89	0.86	0.62	-0.03
	One110c	47	0.85	0.88	0.27	0.04
	One112	44	0.75	0.83	0.23	0.11

Table 1.S1, continued.

	One114	42	0.90	0.89	0.38	0.00
	Ots3	47	0.53	0.55	0.00	0.04
	OtsG68	43	0.84	0.74	0.91	-0.12
	Ots103	47	0.85	0.90	0.23	0.06
	Ots107	45	0.31	0.33	0.49	0.06
Anvil Bay Beach	One100	48	0.79	0.91	0.03	0.14
	One102	48	0.85	0.82	0.84	-0.03
	One103	47	0.96	0.95	0.52	0.00
	One108	48	0.90	0.90	0.55	0.01
	One109	48	0.90	0.85	0.40	-0.04
	One110c	46	0.89	0.89	0.33	0.01
	One112	44	0.86	0.86	0.63	0.01
	One114	37	0.84	0.91	0.08	0.09
	Ots3	48	0.48	0.49	0.39	0.04
	OtsG68	48	0.77	0.70	0.08	-0.09
	Ots103	46	0.91	0.88	0.59	-0.02
	Ots107	48	0.35	0.33	0.78	-0.07
Hidden Lake Creek	One100	47	0.89	0.92	0.11	0.04
	One102	46	0.85	0.82	0.52	-0.02
	One103	46	0.96	0.95	0.39	0.00
	One108	47	0.91	0.91	0.51	0.00
	One109	46	0.89	0.84	0.39	-0.05
	One110c	46	0.85	0.92	0.08	0.09
	One112	47	0.74	0.87	0.01	0.16
	One114	44	0.86	0.91	0.29	0.06
	Ots3	47	0.57	0.57	0.19	0.01
	OtsG68	45	0.71	0.71	0.48	0.02
	Ots103	46	0.83	0.89	0.07	0.09
	Ots107	47	0.23	0.34	0.07	0.33
Lynx Beach	One100	47	0.91	0.92	0.17	0.02
	One102	47	0.81	0.81	0.68	0.01
	One103	47	0.94	0.95	0.43	0.02
	One108	47	0.89	0.90	0.14	0.02
	One109	47	0.83	0.84	0.57	0.02
	One110c	47	0.77	0.89	0.03	0.15
	One112	47	0.85	0.87	0.57	0.03

Table 1.S1, continued.

	One114	47	0.94	0.91	0.81	-0.02
	Ots3	47	0.43	0.41	0.39	-0.04
	OtsG68	47	0.66	0.66	0.51	0.01
	Ots103	47	0.98	0.91	0.99	-0.07
	Ots107	47	0.36	0.32	0.87	-0.11
Lynx Creek	One100	47	0.91	0.92	0.08	0.02
	One102	47	0.81	0.84	0.40	0.05
	One103	47	0.94	0.95	0.19	0.02
	One108	47	0.91	0.89	0.39	-0.01
	One109	47	0.94	0.87	0.87	-0.06
	One110c	47	0.85	0.89	0.24	0.06
	One112	47	0.89	0.86	0.46	-0.03
	One114	47	0.98	0.92	0.96	-0.06
	Ots3	47	0.60	0.50	0.99	-0.18
	OtsG68	47	0.70	0.75	0.25	0.08
	Ots103	47	0.94	0.90	0.81	-0.03
	Ots107	47	0.17	0.18	0.35	0.05
N4 Beach	One100	48	0.96	0.90	0.89	-0.05
	One102	48	0.81	0.83	0.35	0.03
	One103	47	0.96	0.95	0.42	0.01
	One108	48	0.85	0.89	0.05	0.05
	One109	48	0.83	0.81	0.73	-0.01
	One110c	48	0.90	0.91	0.41	0.03
	One112	48	0.90	0.85	0.29	-0.04
	One114	48	0.96	0.91	0.78	-0.04
	Ots3	48	0.50	0.46	0.81	-0.08
	OtsG68	48	0.79	0.73	0.38	-0.07
	Ots103	48	0.83	0.90	0.05	0.09
	Ots107	48	0.38	0.40	0.37	0.07
N4 Creek	One100	48	0.85	0.91	0.02	0.07
	One102	48	0.79	0.72	0.55	-0.09
	One103	48	0.85	0.89	0.13	0.05
	One108	48	0.77	0.85	0.38	0.10
	One109	48	0.77	0.83	0.09	0.08
	One110c	48	0.88	0.87	0.50	0.00
	One112	47	0.74	0.84	0.01	0.13

Table 1.S1, continued.

	One114	48	0.90	0.87	0.77	-0.02
	Ots3	48	0.46	0.41	0.90	-0.10
	OtsG68	48	0.67	0.69	0.46	0.04
	Ots103	48	0.92	0.86	0.84	-0.05
	Ots107	48	0.19	0.27	0.03	0.31
N6 Beach	One100	46	0.89	0.91	0.19	0.03
	One102	46	0.89	0.87	0.27	-0.02
	One103	47	0.96	0.94	0.39	-0.01
	One108	47	0.83	0.87	0.18	0.06
	One109	43	0.84	0.84	0.49	0.01
	One110c	46	0.93	0.90	0.73	-0.02
	One112	46	0.89	0.89	0.77	0.01
	One114	46	0.91	0.91	0.69	0.01
	Ots3	47	0.53	0.48	0.91	-0.10
	OtsG68	47	0.68	0.71	0.22	0.06
	Ots103	46	0.89	0.90	0.39	0.02
	Ots107	46	0.33	0.30	0.84	-0.07
Pick Creek	One100	48	0.81	0.90	0.00	0.11
	One102	47	0.89	0.85	0.61	-0.04
	One103	48	0.96	0.95	0.63	0.00
	One108	47	0.94	0.91	0.26	-0.01
	One109	42	0.83	0.88	0.16	0.07
	One110c	48	0.88	0.90	0.32	0.04
	One112	48	0.83	0.89	0.53	0.07
	One114	48	0.92	0.92	0.47	0.01
	Ots3	48	0.71	0.66	0.88	-0.06
	OtsG68	48	0.63	0.70	0.06	0.11
	Ots103	48	0.92	0.88	0.54	-0.04
	Ots107	48	0.33	0.31	0.82	-0.07
Yako Beach	One100	48	0.79	0.90	0.04	0.13
	One102	48	0.94	0.79	1.00	-0.17
	One103	48	0.94	0.95	0.28	0.02
	One108	48	0.94	0.89	0.79	-0.04
	One109	47	0.89	0.82	0.85	-0.07
	One110c	48	0.83	0.89	0.25	0.07
	One112	48	0.77	0.87	0.02	0.12

Table 1.S1, continued.

	One114	48	0.96	0.92	0.76	-0.03
	Ots3	44	0.57	0.49	0.98	-0.14
	OtsG68	48	0.79	0.72	0.56	-0.09
	Ots103	48	0.92	0.90	0.47	-0.01
	Ots107	48	0.29	0.31	0.37	0.08
Yako Creek	One100	48	0.77	0.91	0.00	0.16
	One102	48	0.88	0.82	0.30	-0.06
	One103	48	0.96	0.95	0.65	0.01
	One108	48	0.85	0.88	0.28	0.04
	One109	48	0.81	0.85	0.19	0.05
	One110c	48	0.94	0.89	0.81	-0.05
	One112	47	0.89	0.87	0.72	-0.02
	One114	48	0.88	0.92	0.12	0.06
	Ots3	48	0.46	0.46	0.52	0.02
	OtsG68	48	0.75	0.71	0.64	-0.04
	Ots103	48	0.88	0.89	0.17	0.02
	Ots107	48	0.29	0.26	1.00	-0.12
Knutson Beach	One100	45	0.53	0.90	0.00	0.42
	One102	46	0.91	0.86	0.67	-0.05
	One103	45	0.82	0.94	0.00	0.14
	One108	46	0.80	0.87	0.04	0.09
	One109	46	0.80	0.86	0.01	0.08
	One110c	46	0.91	0.89	0.52	-0.01
	One112	44	0.93	0.88	0.86	-0.04
	One114	44	0.89	0.93	0.18	0.06
	Ots3	46	0.22	0.20	1.00	-0.07
	OtsG68	46	0.74	0.69	0.76	-0.06
	Ots103	46	0.91	0.93	0.18	0.03
	Ots107	46	0.28	0.25	1.00	-0.11
Knutson Creek	One100	45	0.64	0.91	0.00	0.30
	One102	46	0.93	0.87	0.70	-0.06
	One103	44	0.98	0.92	0.89	-0.05
	One108	46	0.89	0.89	0.21	0.01
	One109	45	0.84	0.86	0.42	0.03
	One110c	46	0.93	0.89	0.09	-0.04
	One112	44	0.98	0.91	0.97	-0.07

Table 1.S1, continued.

	One114	45	0.96	0.93	0.79	-0.01
	Ots3	46	0.24	0.22	1.00	-0.09
	OtsG68	46	0.61	0.67	0.15	0.10
	Ots103	46	0.96	0.91	0.57	-0.04
	Ots107	44	0.27	0.25	1.00	-0.09

Table 1.S2. Pairwise F_{ST} (below diagonal; Weir & Cockerham 1984) and G_{ST} (above diagonal; Nei 1973) comparisons. F_{ST} values significant at the 0.05 level after Bonferroni correction are marked with asterisks.

	AB	AC	CB	CC	EB	EC	ABB	HC	LB	LC	N4B	N4C	N6B	PC	YB	YC	KB	KC
AB	--	0.029	0.012	0.017	0.006	0.007	0.007	0.009	0.011	0.009	0.007	0.016	0.007	0.007	0.010	0.009	0.023	0.022
AC	0.048*		0.035	0.026	0.029	0.034	0.029	0.031	0.029	0.030	0.031	0.037	0.031	0.033	0.031	0.034	0.046	0.045
CB	0.013*	0.062*		0.018	0.013	0.013	0.012	0.015	0.015	0.014	0.011	0.020	0.012	0.014	0.016	0.012	0.025	0.025
CC	0.027*	0.041*	0.027*		0.017	0.018	0.013	0.019	0.017	0.019	0.013	0.029	0.015	0.019	0.017	0.007	0.026	0.029
EB	0.001	0.051*	0.016*	0.024*		0.005	0.007	0.006	0.007	0.007	0.006	0.014	0.006	0.007	0.006	0.006	0.019	0.018
EC	0.004*	0.059*	0.016*	0.025*	0		0.006	0.007	0.009	0.006	0.007	0.016	0.005	0.008	0.007	0.006	0.017	0.016
ABB	0.003	0.051*	0.015*	0.017*	0.003	0.001		0.009	0.007	0.007	0.006	0.016	0.005	0.007	0.008	0.007	0.017	0.017
HC	0.008*	0.055*	0.021*	0.028*	0.002	0.004	0.007*		0.011	0.007	0.007	0.018	0.008	0.007	0.007	0.007	0.018	0.017
LB	0.011*	0.052*	0.021*	0.025*	0.004	0.007	0.005	0.011*		0.009	0.007	0.019	0.008	0.010	0.009	0.009	0.018	0.017
LC	0.006*	0.052*	0.016*	0.024*	0.002	0.000	0.002	0.002	0.006*		0.009	0.017	0.007	0.008	0.008	0.006	0.013	0.014
N4B	0.004	0.051*	0.012*	0.018*	0.001	0.003	0.002	0.003	0.003	0.003		0.016	0.005	0.008	0.006	0.007	0.017	0.018
N4C	0.023*	0.069*	0.031*	0.049*	0.019*	0.022*	0.024*	0.026*	0.030*	0.025*	0.022*		0.016	0.015	0.015	0.014	0.025	0.025
N6B	0.004*	0.055*	0.015*	0.022*	0.002	-0.001	0.000	0.004	0.006*	0.002	-0.001	0.023*		0.007	0.007	0.006	0.014	0.015
PC	0.004*	0.058*	0.017*	0.028*	0.003	0.004	0.003	0.004	0.009*	0.004	0.004	0.021*	0.004		0.009	0.007	0.020	0.020
YB	0.010*	0.055*	0.023*	0.024*	0.001	0.003	0.006	0.002	0.009*	0.004	0.001	0.022*	0.004	0.007*		0.006	0.016	0.016
YC	0.007	0.061*	0.014*	0.029*	0.001	0.002	0.003	0.002	0.008*	0.001	0.001	0.020*	0.001	0.003	0.002		0.014	0.014
KB	0.029*	0.081*	0.037*	0.040*	0.022*	0.019*	0.020*	0.019*	0.023*	0.013*	0.020*	0.041*	0.015*	0.022*	0.019*	0.015*		0.005
KC	0.029*	0.080*	0.038*	0.044*	0.021*	0.019*	0.022*	0.018*	0.023*	0.017*	0.021*	0.040*	0.017*	0.023*	0.019*	0.016*	0.000	

Table 1.S3. Predicted mean trait values for each population, corrected for sampling year, ecotype, site, and ecotype by site effects using ANOVA. FL is female body length, FD is female absolute body depth, FSD is female standardized body depth, ML is male body length, MD is male absolute body depth, and MSD is male standardized body depth.

Site	Ecotype	FL	FD	FSD	ML	MD	MSD
A	Beach	438.2	116.6	155.7	471.2	169.6	155.7
	Stream	426.3	109.3	137.7	437.9	133.4	137.7
C	Beach	437.9	118.4	161.1	474.3	174.5	161.1
	Stream	425.9	94.5	140.6	439.2	136.4	140.6
Elva	Beach	440.4	125.7	178.7	456.4	178.7	178.7
	Stream	416.1	101.1	150.8	456.7	154.4	150.8
Anv/Hidden	Beach	441.1	131.9	172.0	477.8	186.7	172.0
	Stream	421.4	119.4	133.4	430.0	120.8	133.4
Lynx	Beach	440.2	131.1	184.5	472.5	197.7	184.5
	Stream	439.2	97.0	158.5	440.9	164.4	158.5
N4	Beach	449.1	131.1	173.3	495.1	195.4	173.3
	Stream	401.6	129.2	136.7	404.1	124.1	136.7
N6/Pick	Beach	426.6	121.7	161.4	471.3	168.4	161.4
	Stream	441.7	120.6	154.8	470.2	160.9	154.8
Yako	Beach	431.0	121.9	169.0	467.0	177.5	169.0
	Stream	437.0	103.9	138.6	456.9	144.4	138.6
Knutson	Beach	455.1	141.8	162.0	474.0	182.1	162.0
	Stream	443.8	134.5	168.8	469.7	181.9	168.8

Chapter 2: Self-sustaining populations, population sinks, or aggregates of strays: chum (*Oncorhynchus keta*) and Chinook salmon (*O. tshawytscha*) in the Wood River system, Alaska

Published in: Molecular Ecology, 20, 4925-4937

Abstract

Small populations can provide insights on ecological and evolutionary aspects of species distributions over space and time. In the Wood River system in Alaska, USA, small aggregates of Chinook (*Oncorhynchus tshawytscha*) and chum salmon (*O. keta*) spawn in an area dominated by sockeye salmon (*O. nerka*). Our objective was to determine whether these Chinook and chum salmon are reproductively isolated, self-sustaining populations, population sinks that produce returning adults but receive immigration, or strays from other systems that do not produce returning adults. DNA samples collected from adult chum salmon from 16 streams and Chinook salmon from 4 streams in the Wood River system over three years were compared to samples from large populations in the nearby Nushagak River system, a likely source of strays. For both species, microsatellite markers indicated no significant genetic differentiation between the two systems. Simulations of microsatellite data in a large source and a smaller sink population suggested that considerable immigration would be required to counteract the diverging effects of genetic drift and produce genetic distances as small as those

observed, considering the small census sizes of the two species in the Wood River system. Thus, the Wood River system likely receives substantial immigration from neighboring watersheds, such as the Nushagak River system, which supports highly productive runs. Although no data on population productivity in the Wood River system exist, our results suggest source-sink dynamics for the two species, a finding relevant to other systems where salmonid population sizes are limited by habitat factors.

Introduction

Many species exist as populations that differ greatly in abundance, and examination of the small populations can provide insights into basic ecological and evolutionary processes determining species distributions and abundances. Small populations may be self-sustaining in habitats with low carrying capacity, population sinks where reproduction occurs but at levels too low to be self-sustaining and requiring immigration to persist, or aggregates of individuals in unsuitable habitats that have immigrated from other areas but do not reproduce successfully. Small populations are important to conserve because they may represent an important component of biocomplexity in natural systems (Rogers & Schindler 2008), contributing to intraspecific variation and resilience of the species as a whole.

The contribution of small populations to species stability is especially relevant in the context of metapopulations and source-sink dynamics. If productivity varies among demes, dispersal may occur from source populations (net exporters of individuals), to sink populations (net importers; Pulliam 1988). Although large populations commonly act as sources and small ones as sinks (Palstra *et al.* 2007), estimates of dispersal rates are

necessary to confirm source-sink dynamics, since abundances alone do not show whether demographic supplementation is important for persistence (Cooper & Mangel 1999). Tagging studies can provide estimates of movement among populations, but they cannot determine whether the dispersers successfully reproduce. In contrast, genetic data measure gene flow among populations (either past or present, depending on colonization history and method used) and offer additional insight into source-sink dynamics in wild populations (Lowe & Allendorf 2010).

In addition to its demographic effect, dispersal permits gene flow and therefore affects local adaptation and species' range limits (Sexton *et al.* 2009). Broadly speaking, gene flow tends to homogenize genetic diversity between populations, whereas natural selection and local adaptation lead to population divergence (Garant *et al.* 2007). This balance between local adaptation and gene flow may determine whether small populations are self-sustaining units or sinks. High immigration rates into such sink populations may prevent local adaptation, thereby reducing population fitness and self-recruitment and further increasing reliance on immigration, in a process termed gene swamping (Bridle & Vines 2007) or migrational melt-down (Ronce & Kirkpatrick 2001). These processes are especially relevant in species subject to human exploitation in addition to natural mortality, as population diversity (Hilborn *et al.* 2003) may be critical to sustain harvest, and levels of productivity that would be sufficient for sustainability in the absence of exploitation might be insufficient once exploitation occurs.

Pacific salmon show considerable intraspecific genetic and phenotypic variation, and are an excellent taxon for investigating the evolutionary consequences of source-sink

dynamics. They occur in spawning groups that are largely isolated due to homing behavior, yet still demographically connected through low levels of straying, or dispersal of mature individuals to breed in non-natal habitats (Hendry *et al.* 2004b; Quinn 1993; Schtickzelle & Quinn 2007). Spawning population sizes also vary and can be quite small (Esin & Leman 2008; Scarnecchia & Roper 2000). Population persistence typically relies on the relationship between local adaptation and habitat characteristics (Allendorf & Waples 1996), and thus studying small or marginal populations where persistence is uncertain can contribute to our understanding of species ecology.

The Wood River system in southwestern Alaska, USA, is an ideal location for conducting research on natural small populations of wild salmonids, in part because the spawning habitat is unaltered by human activities, and all salmon are wild (i.e., no artificial production). Sockeye salmon are numerically dominant in the system and have been the primary research focus because of their commercial importance, but there are small numbers of individuals from other salmon species, including chum (*O. keta*) and Chinook salmon (*O. tshawytscha*). Survey data for 15 streams were consistently collected by the Fisheries Research Institute (FRI) at the University of Washington from 1968 to 2007. These data showed low population densities and census sizes for chum and Chinook salmon; many streams had no recorded observations, and streams with observations averaged fewer than 5 individuals per km of habitat (Pess 2009). FRI has also regularly seined 10 beach sites from June to August within Lake Aleknagik, the lowermost lake of the Wood River system, since 1963 (methods described in Rogers 1973). Juvenile chum and Chinook salmon have been caught occasionally (40% of years

for chum salmon, 85% of years for Chinook salmon), indicating successful reproduction in the system. These juveniles almost certainly did not originate from other watersheds because juvenile chum salmon migrate directly to sea in their first year (Quinn 2005) and would not swim > 30 km up the Wood River to Lake Aleknagik if they encountered the river on their downstream migration from other systems. Juvenile Chinook salmon sometimes move into non-natal tributaries for temporary foraging (e.g. Murray & Rosenau 1989), but as with the chum salmon, it is highly unlikely that they would ascend the Wood River to enter Lake Aleknagik from the confluence with the Nushagak River (Fig. 2.1). Analyses suggest that the distribution and abundance of these two species in the Wood River system is affected primarily by habitat factors (watershed drainage area, stream depth), and to a lesser extent, sockeye salmon densities (Pess 2009). However, the status of these chum and Chinook salmon populations is unknown; specifically, whether they are self-sustaining populations, population sinks demographically sustained by immigrants from other systems, or aggregates of strays.

The Wood River flows into the lower part of the Nushagak River (Fig. 2.1), and the Nushagak River and its other tributaries are the most likely sources of strays into the Wood River system because they have large spawning populations of chum and Chinook salmon. Alaska Department of Fish and Game (ADF &G) records show that annual escapements have numbered in the tens thousands for Chinook salmon and in the hundreds of thousands for chum salmon from 1990-2009 (Fig. 2.1; Morstad *et al.* 2010). Spawning and rearing distributions have been documented in the Nushagak River system (ADF &G 2011; Johnson & Blanche 2010), and population productivity is sufficient to

support commercial fisheries for both chum and Chinook salmon (Baker *et al.* 2006; Kendall & Quinn 2009). Other potential source populations of Chinook salmon include the Togiak, Naknek, Alagnak, and Egegik river systems (Baker *et al.* 2006), but these systems are quite geographically distant in comparison, and straying tends to decrease rapidly with distance (Pascual & Quinn 1994).

We used molecular genetic (microsatellite markers) and demographic data to examine the population structure of chum and Chinook salmon in the Wood River system and determined their relationship to chum and Chinook salmon in the Nushagak River system. We hypothesized that the small Wood River system populations should accumulate detectable genetic differentiation within a few generations if they were reproductively isolated and self-sustaining, whereas substantial straying from neighboring populations should homogenize allele frequencies. To distinguish these hypotheses, we used computer simulations to explore the range of possible scenarios of sink population size and immigration rates, given observed levels of genetic differentiation and assuming recent divergence. Although we lacked the detailed demographic data required to directly demonstrate source-sink dynamics (population growth rates or density-dependent effects associated with dispersal;Pulliam 1988; Watkinson & Sutherland 1995), our results provide evidence for the importance of population sources and sinks in chum and Chinook salmon.

Materials and methods

Fish were sampled in streams and rivers throughout the Wood River system, which is comprised of a series of lakes (Fig. 2.1). All tissue samples were taken non-

lethally from fish caught by hook and line, and subsequently preserved in 95%-100% ethanol. In total, 242 chum salmon from the Wood River system were sampled over 3 years (2004-2006) from 16 locations (Table 2.1). Sample sizes ranged from 1-46 individuals per site per year. For Chinook salmon, 41 fish were sampled over the same three years from 4 locations (Table 2.2), with sample sizes ranging from 1-27 individuals per site per year.

For genetic comparison, tissues were also collected in 2006 from salmon collected at counting towers on the Nushagak River. The Wood River enters the Nushagak River near its mouth, making the Nushagak River system a likely source of strays. The Nushagak River system samples were collected in June and July to increase sampling coverage of adults arriving at different times (Tables 2.1 and 2.2). Samples of chum and Chinook salmon were also obtained from two Yukon River populations (the Chandalar and Andreafsky rivers; Fig. 2.1) to be analyzed as outgroups because they are spatially distant from the Wood and Nushagak river systems (Fig. 2.1). Moreover, the Chandalar River salmon return later in the year to spawn (fall run), whereas the Andreafsky, Nushagak, and Wood river salmon are summer runs. Sample sizes ranged from 22-48 per location per species, and sampling occurred between 2001-2004 (Tables 2.1 and 2.2).

Microsatellite analysis

DNA was extracted from the fin tissues using Qiagen DNeasy kits, following the manufacturer's protocols. For chum salmon, nine tetranucleotide repeat microsatellite loci and four dinucleotide repeat loci were used to analyze genetic variation: *One101, One103, One106, One111, One114* (Olsen et al. 2000), *Ots3* (Banks *et al.* 1999), *Ots103*

(Beacham *et al.* 1998), *Oke4, Oke8, Oke11* (Buchholz *et al.* 2001), *Oki1 Lower, Oki1 Upper,* and *Oki23* (Smith *et al.* 1998). Eleven microsatellite loci were used to analyze the Chinook salmon samples, eight with tetranucleotide repeats and three with dinucleotide repeats: *Ogo2*, *Ogo4* (Olsen *et al.* 1998), *Oki100* (K.M. Miller, DFO, Canada, unpublished data), *Omm1080* (Rexroad *et al.* 2001), *Ots208b*, *Ots212*, *Ots213* (Greig *et al.* 2003), *Ots3M*, *Ots9* (Greig & Banks 1999), *OtsG474* (Williamson *et al.* 2002), and Ssa408UOS (Cairney *et al.* 2000).

Each polymerase chain reaction (PCR) was carried out in a 10µl reaction volume comprised of 1µl of extracted DNA, 1.5mM $MgCl_2$, 0.8mM dNTPs, 2µM of each primer, and 0.5 Units Taq DNA polymerase (Taq DNA Polymerase, Gene Choice). A touchdown PCR was used, with 6 cycles of 1-min at 95ºC, 30-sec at 61 °C (-1 °C /cycle), and 15-sec at 72 °C (15s), followed by 22 cycles with the annealing step at 56 °C, and a final extension time of 20 min at 72ºC. All forward primers were labeled with fluorescent dye, and the labeled PCR fragments were size-separated on an automated DNA sequencer (Megabace 1000, Amersham Biosciences) with appropriate size standards. Allele fragment size estimates were obtained using Genetic Profiler genotyping software (v2.2, Amersham Biosciences). MICROCHECKER (van Oosterhout *et al.* 2004) was used to check for evidence of null alleles or genotyping error due to stuttering. Genotype frequencies were tested for departures from Hardy-Weinberg equilibrium and linkage equilibrium with GENEPOP 4.0.10 (Raymond & Rousset 1995), based on Guo and Thompson (1992). Genotypic population differentiation was determined by GENEPOP as well. FSTAT (Goudet 1995) was used to calculate and test significance of overall and

pairwise F_{ST} values (Weir & Cockerham 1984), and to estimate allelic richness (El Mousadik & Petit 1996). Samples with fewer than 10 individuals were not included in the allelic richness calculations in order to avoid bias (Leberg 2002). Expected heterozygosities were calculated in GENALEX (Peakall & Smouse 2006). LDNE (Waples & Do 2008) was used to estimate effective population sizes (N_e) from linkage disequilibrium between loci. The program STRUCTURE V.2.3.3 (Falush *et al.* 2003; Pritchard *et al.* 2000) was used to cluster individuals into putative populations based on both genetic data and information on sampling location (Falush *et al.* 2007; Hubisz *et al.* 2009). Arlequin v. 3.5 (Excoffier & Lischer 2010) tested for genetic differentiation among groups of samples by analysis of molecular variance (AMOVA), including groups by lake (within the Wood River system) and by watershed. Relatedness was assessed within collections (IDENTIX; (Belkhir *et al.* 2002) and between individuals (ML-RELATE; (Kalinowski *et al.* 2006). IDENTIX can calculate overall relatedness within a sample and compare the result against random expectations, whereas ML-RELATE estimates pairwise relatedness and the most likely relationship between individuals. For the ML-RELATE analysis, relatedness summaries were calculated for relationships between: 1) individuals collected at the same site in the same year and 2) individuals collected at different sites and/or years. The genetic assignment software GENECLASS2 (Piry *et al.* 2004) determined whether individuals could be excluded from the Yukon and Nushagak river population samples based on the criteria of Cornuet *et al*. (1999) and Rannala and Mountain (1997).

Simulations

Power analyses were carried out in the program POWSIM (2006) to determine the power of the chum and Chinook salmon microsatellite marker sets to detect genetic differentiation as measured by F_{ST}. Genetic drift was simulated to produce the low observed F_{ST} values (0.003-0.004) between two populations with effective sizes of 1000 each, based on empirical allele frequencies in the marker set being tested. Sample sizes of 10 and 20, roughly corresponding to the Wood River system collections, were then simulated and analyzed using Fisher's exact test to estimate the power of those sample sizes to detect the genetic differentiation.

To consider source-sink dynamics, NEMO 2.1.3 (Guillaume & Rougemont 2006) was used to test how immigration rates and proportion of dispersers within a sink population would affect the extent of genetic differentiation from a source population. NEMO is a stochastic, individual-based, forward-time model that can simulate various demographic processes, including movement of individuals between populations. In the model, adults mated and produced offspring, which matured and dispersed from the source to the sink population with some probability. During the "aging" process, all adults were removed (because Pacific salmon are semelparous: Quinn 2005), and offspring were randomly culled from the sink so that its size remained constant and did not exceed the defined carrying capacity. The remaining individuals in each population then bred, continuing the life cycle.

Two populations were modeled for each run: a sink population of varying carrying capacity from 50-200 individuals, and a source population with a carrying

capacity of 5000 individuals. According to Wood River system survey data, the longest stream with the highest densities of chum and Chinook salmon (3 fish per km) was Ice Creek, which includes approximately 16 km of spawning habitat (Marriott 1964). The range of sink carrying capacities for the simulations was chosen to include estimates of maximum census sizes based on this information. The carrying capacity of the source population was considered a minimum estimate for the census sizes of these species in the Nushagak River (Fig. 2.2). Data were simulated for 10 unlinked (recombination rate set at 0.5) neutral loci with an average of 10 alleles per locus, so that the simulated data would resemble the empirical data collected at 10 microsatellite loci. A single step mutation model was implemented with mutation rate 10^{-5}. To consider the effect of dispersal on population differentiation, the proportion of immigrants in the sink population was varied from 0 to 0.5, and F_{ST} values (Weir & Cockerham 1984) were recorded every 10 generations. 1000 replicates were simulated for each specific combination of parameter values.

To consider the explicit relationship between immigration rate and F_{ST} for specific combinations of sink population size and generations since divergence, curves were fit to data from the NEMO simulations using the curve-fitting tool http://www.zunzun.com. First, appropriate functions were found using the function finder (ranked by lowest squared sum of absolute error), and then the best-fitting functions were used to calculate the immigration rate required to achieve the empirically observed overall F_{ST} values for chum and Chinook salmon. The best fitting curve for most parameter combinations took the form $y = a^{\ln(bx + c)}$, where a, b, and c were coefficients

estimated for each data set, x was the immigration rate, and y was the F_{ST} value. When only one generation had passed since divergence, the data curves looked substantially different and fit well to curves of the form $y = a^x + b$.

Results

Microsatellite analysis

The expected heterozygosities of chum salmon microsatellite loci ranged from 0.098 (*Oke8*) to 0.917 (*One111*), with 3 – 77 alleles per locus. Two loci, *One106* and *Oki23*, deviated significantly from Hardy-Weinberg equilibrium ($P < 0.0001$) and were consequently excluded from further analysis, although MICROCHECKER found no evidence for null alleles, stuttering, or large allele dropout. Linkage disequilibrium tests indicated that the loci *One101* and *One103* were completely correlated, and *One103* was therefore dropped as well. All subsequent analyses were conducted using the remaining 10 loci. The Chinook salmon microsatellite loci also differed in variability; expected heterozgosity ranged from 0.13 (*OtsG474*) to 0.93 (*Ots208b*) and 4-38 alleles per locus. Loci showed no evidence of correlation or Hardy-Weinberg disequilibrium, although the Nushagak River sample had more linkage disequilibria than expected (9 of 66 pairwise comparisons were significant; $P < 0.05$).

Genetic diversity within chum salmon samples was relatively low (mean expected heterozygosity = 0.57) and similar among collections of two individuals or more. Notably, the heterozygosity and allelic richness values from the small collections in the Wood River system were similar to those of the large populations in the Nushagak and Yukon river systems (Table 2.1). The overall F_{ST} was low (F_{ST}=0.005) but significant

(P=0.03). Differentiation was primarily due to the Chandalar River sample, which was the only fall run sample in the collection. Pairwise F_{ST} values between the Chandalar River and other samples were all statistically significant, with P values ranging from 0.013-0.047 (Table 3). Elva Creek fish collected in 2005 also were genetically different from some other samples (Table 2.3). Excluding the geographically distant Andreafsky and Chandalar river samples, the overall F_{ST} decreased to 0.003 but was still significant (P = 0.025).

The Chinook salmon microsatellite loci were slightly more variable than the chum loci with a mean expected heterozygosity of 0.63. Again, some of the small collections in the Wood River system, such as Elva and Ice creeks, had heterozygosities and allelic richnesses similar to those observed in the large Nushagak and Yukon river populations (Table 2.2). The overall F_{ST} was greater than that for chum salmon (F_{ST} = 0.009) and highly significant (P < 0.001), the significance driven by the genetic differentiation between the Chandalar population and the rest of the collections. Pairwise F_{ST} values among most of the samples were small and not statistically significant, except for comparisons involving the Chandalar River (Table 2.4). Excluding the Andreafsky and Chandalar river samples, overall F_{ST} decreased to 0.004 but was still statistically significant (P = 0.034). Importantly, the observed differentiation of the Chandalar River samples demonstrated that marker sets for both species were adequate to detect genetic differentiation among samples, despite the small sample sizes.

Clustering approaches revealed no genetic structure for either species. STRUCTURE was unable to infer distinct populations for chum or Chinook salmon, even

using approaches allowing for null alleles and prior information on sampling location. Additionally, AMOVA in ARLEQUIN indicated no genetic differentiation among the Wood River system lakes or among watersheds. GENECLASS 2 was unable to exclude individuals sampled in the Wood River system from the Yukon and Chandalar river populations with greater than 0.95 probability. LDNE was unable to estimate effective population sizes (N_e) for most samples, and even when a finite point estimate was obtained, the upper confidence interval was always infinitely large. The inability to estimate N_e was not due solely to small sample sizes. When data from all the Nushagak River system samples were combined for each species (N = 95 for chum salmon, N = 49 for Chinook salmon), upper confidence limits were still infinitely large.

Tests for relatedness within collections (IDENTIX) failed to reveal significantly higher relatedness than expected by chance in any of the collections. Estimates of relatedness between individuals (ML-RELATE) told a similar story, as individuals collected at the same site in the same year did not have higher mean relatedness than individuals collected at different sites and years.

Simulations

POWSIM determined that both the chum and Chinook salmon microsatellite marker sets had moderate power to detect low F_{ST} values when sample sizes were small. The chum salmon marker set with 10 loci could detect a significant ($P < 0.05$) F_{ST} value of 0.003 with 40% power, assuming a sample size of 20. Power dropped to 20% when the sample size was reduced to 10 individuals. The Chinook salmon 11 marker set could detect a significant ($P < 0.05$) F_{ST} value of 0.004 with 49% power, assuming a sample

size of 20, and power decreased to 27% for a sample size of 10. As limiting analysis to samples of size 20 or greater considerably reduced the number of collections that could be included, a cut-off sample size of 10 was used to construct the pairwise F_{ST} tables (Tables 2.3-2.4) despite the reduced power for the smaller samples.

Simulations in the program NEMO indicated that smaller populations diverged more quickly and to a greater extent than larger populations, assuming equivalent immigration rates. Immigration rate was defined as the proportion of the recipient population comprised by strays from the source population. For the range of parameter values tested (N_e ranging from 50-200, immigration rates ranging from 0.01 to 0.5), F_{ST} values stabilized by approximately 150 generations. To achieve an F_{ST} value similar to the overall F_{ST} observed empirically in chum salmon ($F_{ST} \sim 0.003$) in a population size of 50, NEMO indicated that the recipient population needed an ongoing immigration rate of 0.50 or greater, assuming at least 10 generations had passed since population divergence (Fig. 2.3). For Chinook salmon, the ongoing immigration rate needed to be 0.45 or greater (Fig. 2.4). Assuming extremely recent divergence (one generation of reproduction since separation from the source population), even zero immigration would not have resulted in F_{ST} values as high as those observed if the sink N_e was 200 (Fig. 3). Those F_{ST} values could have been observed after one generation if N_e was 50 or 100, however. If N_e was 50, the immigration rate would have to be 0.48 to achieve F_{ST} values as low as those observed for chum salmon, and 0.36 to achieve F_{ST} values as low as those observed for Chinook salmon. Those immigration rates would decrease to 0.24 and 0.11, respectively, if N_e was 100.

Discussion

For both chum and Chinook salmon, most collections from the Wood River system were neither differentiated from each other nor from potential source populations in the nearby Nushagak River system (Tables 2.3 and 2.4). The collections did differ from the Chandalar River sample, which was fall run (Tables 2.3 and 2.4), suggesting that different run times isolate populations more than geographic separation, a conclusion supported by prior research (Gharrett *et al.* 1987; Varnavskaya *et al.* 1994; Wilmot *et al.* 1994). However, the general lack of genetic differentiation of the Wood River system Chinook and chum salmon spawning aggregates was somewhat unexpected considering their small census sizes. If these small collections were self-sustaining and at least somewhat reproductively isolated, they should have been strongly influenced by genetic drift and genetically diverged within a few generations (Fig. 2.5). Three factors would have affected the extent of divergence: effective population size (N_e), time since separation from the source population, and immigration rate.

Populations with small effective sizes diverge more quickly than larger populations, and each of the Wood River system streams likely had a population size of less than 100 individuals based on field observations of their absolute numbers, which averaged fewer than 10 individuals per km of habitat (Pess 2009). Process and observation error associated with visual surveys may have biased our estimates of Wood River system chum and Chinook salmon population sizes downward (see Jones *et al.* 1998). Chum and Chinook salmon are larger-bodied and have distinct coloration from sockeye salmon, making them noticeable in the field, but they would have been missed if

they arrived after the surveys. Post-survey arrivals undoubtedly occurred to some extent but were not a systematic source of error, because the spawn timing of these species is similar to that of sockeye salmon, the primary target of the surveys (ADF &G unpublished data). Unfortunately, the genetic data were insufficient for providing estimates of N_e for each collection. Although N_e is typically less than census size in wild populations (Frankham 1995), any immigration will inflate N_e estimates, and the fact that our estimates effectively had no finite confidence limits suggested that these fish were part of a larger population that included fish originating from other sites.

Increasing time since population divergence will increase genetic differentiation, until migration-drift equilibrium, a state in which the diverging effect of genetic drift and the homogenizing effect of migration (dispersal) are balanced, is reached. The time required to reach this equilibrium varies with population size and dispersal rate but may be on the order of 600 generations to reach 95% of the equilibrium F_{ST} value, assuming an effective population size of 100 (Whitlock & McCauley 1999). The Wood River system collections have been evolving over no more than the last 10,000 years, as salmon could only have colonized the era following the last Pleistocene glaciation (Manley *et al.* 2001). Assuming a generation time of 5 years for chum and Chinook salmon (Quinn 2005), approximately 2000 generations have passed, suggesting that the collections could be at equilibrium. However, extinction and re-colonization events may have occurred since the last glaciers receded, and as exact estimates of time since divergence could not be made, assuming recent divergence was the most conservative approach.

Combining our conjectures on N_e and time since divergence for the Wood River system collections, we estimated lower bounds of ongoing immigration rates based on simulations in NEMO and the estimates of F_{ST} from the microsatellite data. First, the possibility that the collections were reproductively isolated could be eliminated, as simulations projected that a population of 100 individuals would undergo substantial genetic divergence (F_{ST} = 0.005, significant according to POWSIM) after only one generation of reproductive isolation (Fig. 2.5), greater than what was observed in the data (overall F_{ST} = 0.003 for chum salmon and 0.004 for Chinook salmon). To achieve the observed genetic differentiation after one generation of divergence, an immigration rate of 0.2 would be required for chum salmon and 0.1 for Chinook salmon. Much higher immigration rates would have been required if 10-150 generations had passed since divergence, on the order of 0.35 or greater for both species (Figs. 2.3 and 2.4). Taken together, the empirical and simulation data indicated that the Wood River system spawning aggregates were at least partially comprised of immigrants and are not isolated populations, even allowing for the possibility that they have only recently diverged.

One alternative explanation for the observed results is that sufficient gene flow occurs among Wood River system locations such that the entire system effectively comprises a single larger population that is less affected by genetic drift. However, AMOVA showed no genetic differentiation between the grouped Wood River system samples and any of the other watersheds. Even if some straying occurs among Wood River system sites, at least some individuals are likely immigrants from neighboring systems that have much higher population sizes and densities of these species, especially

the Nushagak River system. Given that the Nushagak River system chum and Chinook salmon escapements can each number in the tens to hundreds of thousands every spawning season (Fig. 2.2; Kendall & Quinn 2011; Morstad *et al.* 2010), straying rates as low as 1-5% could easily have resulted in the numbers of fish that were observed at all the Wood River system sites.

Nevertheless, the idea that all the Wood River chum and Chinook salmon were strays was not supported by demographic data. Some sites, such as Hidden Lake Creek and Whitefish Creek, had very low observed abundances and occurrence of these species, with chum and Chinook salmon being observed during fewer than 10% of stream surveys over 35 years (Pess 2009). These particular streams probably lacked spawning populations and simply received strays from time to time. However, other sites, notably Ice Creek, had much higher occurrence and abundances of these species (Pess 2009), suggesting persistent populations.

For chum salmon, adult demographic data indicated potential populations in several streams. Fenno, Ice, and Pick creeks had relatively consistent observations of this species ($\geq$ 50% of annual surveys), and overall chum salmon occurrence increased over time from 8% of surveyed streams in the 1970s to 44% by the 2000s (Pess 2009). There was also direct evidence for local reproduction, as beach seines in Lake Aleknagik captured juvenile chum salmon in 15 of 40 years, including the years 2006-2009. The inconsistency of chum salmon catches may be explained by the fact that chum salmon migrate to sea during their first summer (Salo 1991), making them challenging to detect because they stay in the system only briefly and are easily missed in weekly sampling at

selected sites in a large lake. Additionally, juvenile chum salmon closely resemble the much more numerous juvenile sockeye salmon, and some may have been mis-identified, creating a downward bias in their estimated numbers.

Interestingly, the Elva Creek 2005 chum salmon sample differed genetically from 7 of the 13 other samples with 10 or more individuals (Table 2.3; average pairwise F_{ST} = 0.0083), indicating some degree of reproductive isolation. However, there was no evidence for higher relatedness or linkage disequilibrium within Elva Creek, which might be expected if there was at least one generation of successful reproduction in the stream. Demographic data also showed generally low occurrence (20% of annual surveys) and abundance of chum salmon in Elva Creek (Pess 2009). Thus, the cause of slight genetic differentiation of the Elva Creek 2005 sample was unclear, and additional sampling may help determine whether the site sustains a population.

For Chinook salmon, demographic data suggested a potential population in Ice Creek, a tributary with relatively deep water and pools that make it more suitable for spawning by the large-bodied Chinook salmon than the other, smaller streams. Among the Wood River system streams, Ice Creek had the highest reported abundance (193 individuals observed over 35 years) and occurrence (proportion of years observed; 39%) of Chinook salmon (Pess 2009). Nesting behavior was observed in the stream during sampling, and beach seines regularly captured juvenile Chinook salmon in Lake Aleknagik downstream. Ice Creek may therefore harbor a population that reproduces successfully but receives sufficient gene flow from outside sources to prevent genetic divergence.

In summary, our data indicate that at least some of the Wood River system chum and Chinook salmon receive strays from outside sources, most likely the adjacent and highly productive Nushagak River system, and may act as population sinks. However, we were unable to establish whether these populations depend entirely on immigration to persist (absolute sinks; Kawecki 2008) or whether immigration only boosts abundances (relative or pseudo-sinks; Watkinson & Sutherland 1995). Estimates of birth and death rates would indicate whether reproduction is sufficient for balancing mortality (Pulliam 1988), but density dependent effects may decrease birth and increase mortality rates, causing mimicking of true sink behavior (Watkinson & Sutherland 1995). Such effects are unlikely in Wood River chum and Chinook salmon due to their low densities. Experimental manipulations, such as artificially altering densities or isolating populations, could demonstrate whether a potential sink population actually depends on dispersal for persistence (Watkinson & Sutherland 1995) but are entirely unfeasible in wild anadromous salmon in Alaska. Nevertheless, although such ultimate demographic demonstration of sink populations were outside the scope of this project, the genetic data and associated simulations represent direct evidence of source-sink dynamics in salmonid species. Our findings are also relevant for other systems where habitat degradation and other factors may lead to population declines and source-sink behavior (e.g. Bradford & Irvine 2000) and where maladaptation at range margins limits species distributions (Kawecki 2008).

Ecological data were consistent with the possibility that the Wood River system includes sink populations of chum and Chinook salmon. Spawning habitat in the Wood

River system is sub-optimal because many streams are too shallow for these large-bodied fish (Pess 2009), and so these populations are probably not very productive and receive far more strays than they contribute to other systems. This high immigration rate, in turn, may prevent local adaptation to these habitats by constant influx of maladaptive genes and thus the establishment of self-sustaining populations (Mayr 1963; Sexton *et al.* 2009) in a process of 'migration meltdown' (Ronce & Kirkpatrick 2001). Alternatively, the Wood River system may harbor pseudo-sink populations that are self-sustaining but still receive immigration. However, although pseudo-sinks likely include a lower proportion of immigrant genes than true sinks, the substantial gene flow indicated by our results would still potentially limit local adaptation.

The potential source-sink dynamics indicated here become even more intriguing when considering fishing pressure on these populations. The Chinook salmon fishery in the Nushagak fishing district, which includes fish from both the Wood and Nushagak river systems, takes about 50% of the returning adults (Kendall & Quinn 2011), such that a population needs to average two recruits per spawner to maintain the population. Without the fishery, populations that currently produce fewer than two recruits per spawner may be self-sustaining or even source populations. Exploitation may therefore favor highly productive populations and tend to reduce or eliminate less productive ones, altering source-sink dynamics and potentially shifting the balance between local adaptation and gene flow. Such changes may limit population maintenance and colonization in less productive habitats. Despite the interest in fishery-induced evolution (Kuparinen & Merila 2007), this aspect of population diversity and productivity in

exploited species has found little attention so far, though it may have substantial impacts on species sustainability (Hilborn *et al.* 2003; Schindler *et al.* 2010).

Regardless of the specific mechanism limiting their abundances, the peripheral status of chum and Chinook salmon in the Wood River system may change in the future. Environmental conditions in the system may shift so that habitat suitability increases for these species, and the populations may also evolve and increase local adaptation given adequate genetic variation and selection pressures (Kawecki 2008). Any resulting changes in productivity and the direction of gene flow among populations can have important implications for species resilience and range expansion (Kawecki 2008; Palstra *et al.* 2007), including the possibility of sink populations becoming sources (Dias 1996). Thus, despite their currently low numbers, the Wood River system chum and Chinook salmon may eventually contribute to the productivity of their respective species, a possibility that should be considered in management.

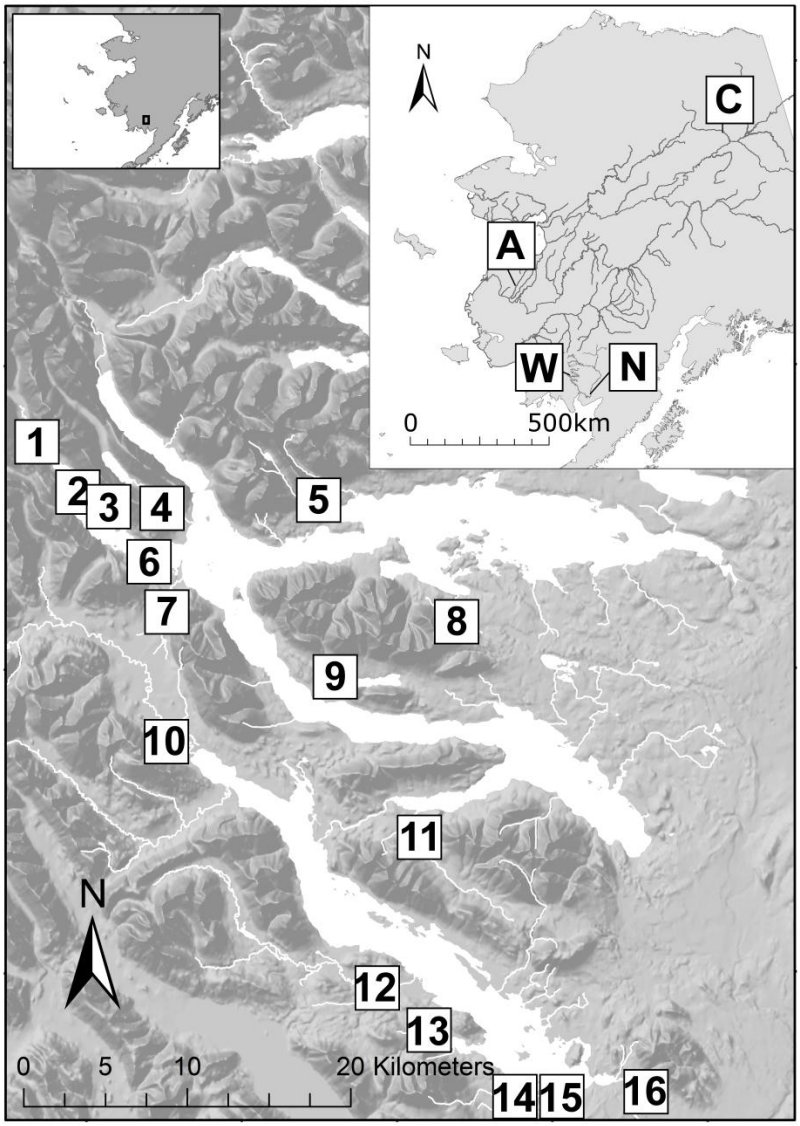


Figure 2.1. Map of the Wood River Lakes system and sampling locations for chum and Chinook salmon: A=Andreafsky River, C=Chandalar River, W=Wood River system, N=Nushagak River. Sampling sites within the Wood River system are: 1=Little Togiak Creek, 2=C Creek, 3=A Creek, 4=Elva Creek, 5=Joe Creek, 6=Little Togiak River, 7=Pick Creek, 8=Hidden Lake Creek, 9=Lynx Creek, 10=Sunshine Creek, 11=Fenno Creek, 12=Ice Creek, 13=Bear Creek, 14=Yako Creek, 15=Whitefish Creek, 16=Wood River.

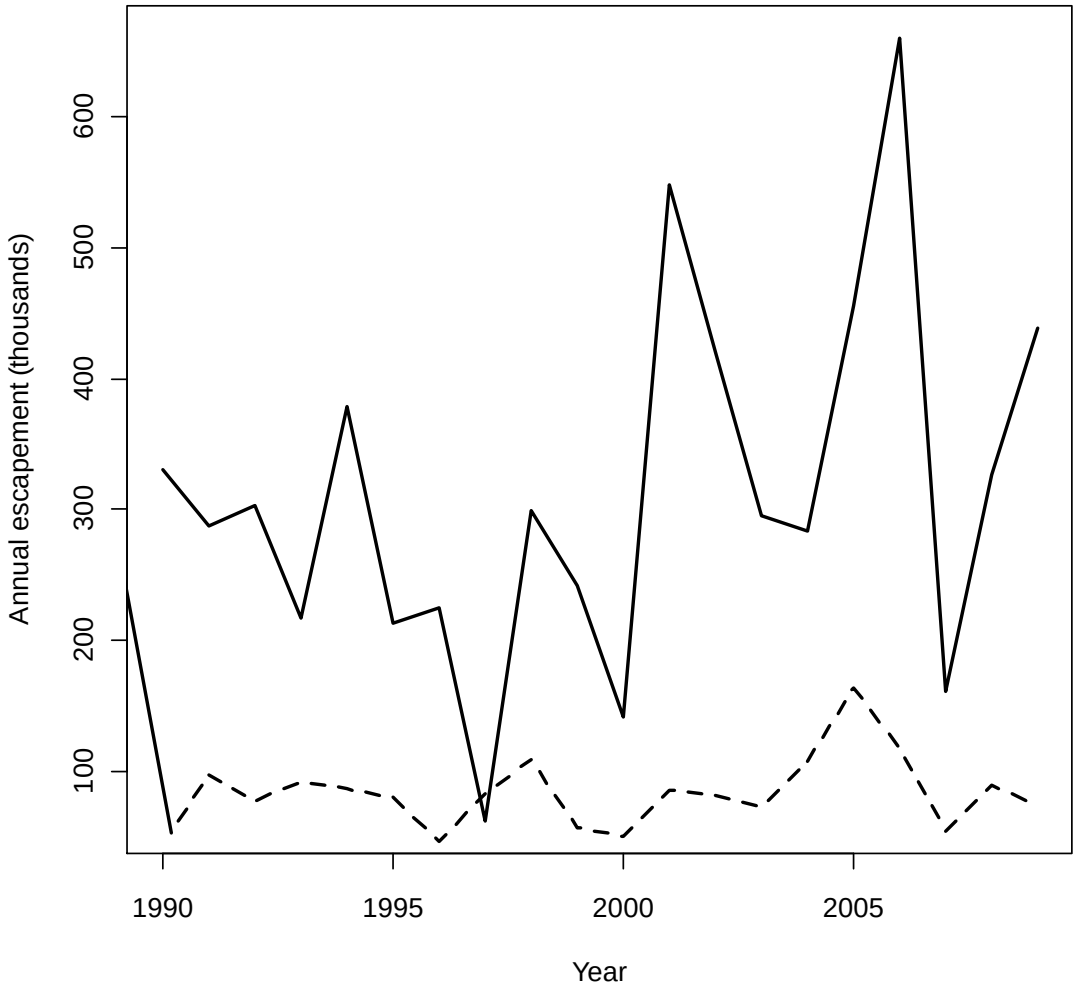


Figure 2.2. Chum (solid line) and Chinook (dashed line) salmon escapements to the Nushagak River system from 1990-2009.

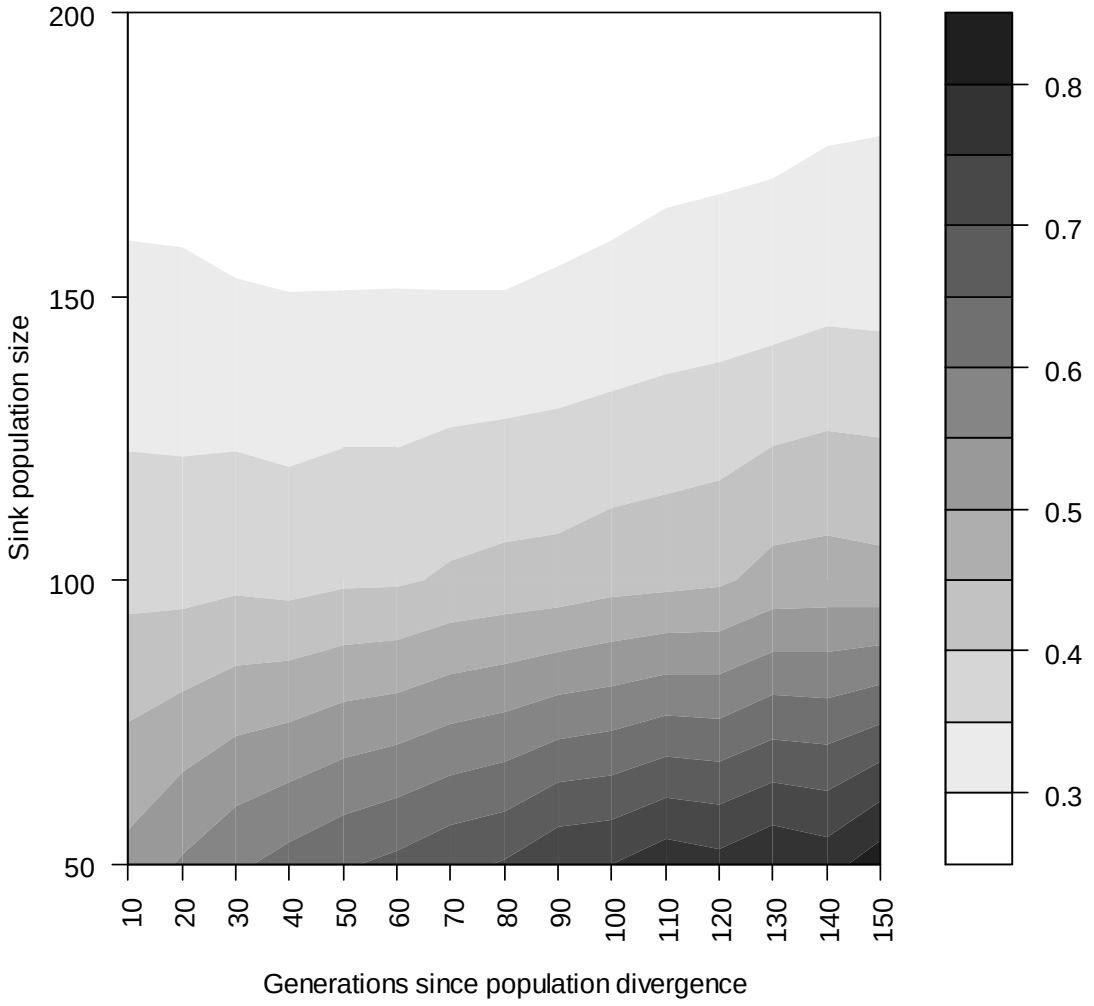


Figure 2.3. Contour plots of ongoing immigration rates required to produce a specific F_{ST} value between a simulated source and sink population, assuming different combinations of: 1) sink effective population size and 2) generations since the sink population split from the source population. The different shades represent different categories of immigration rates, with darker shades representing higher immigration rates. This figure is for an F_{ST} of 0.003, equivalent to the empirical value observed for chum salmon.

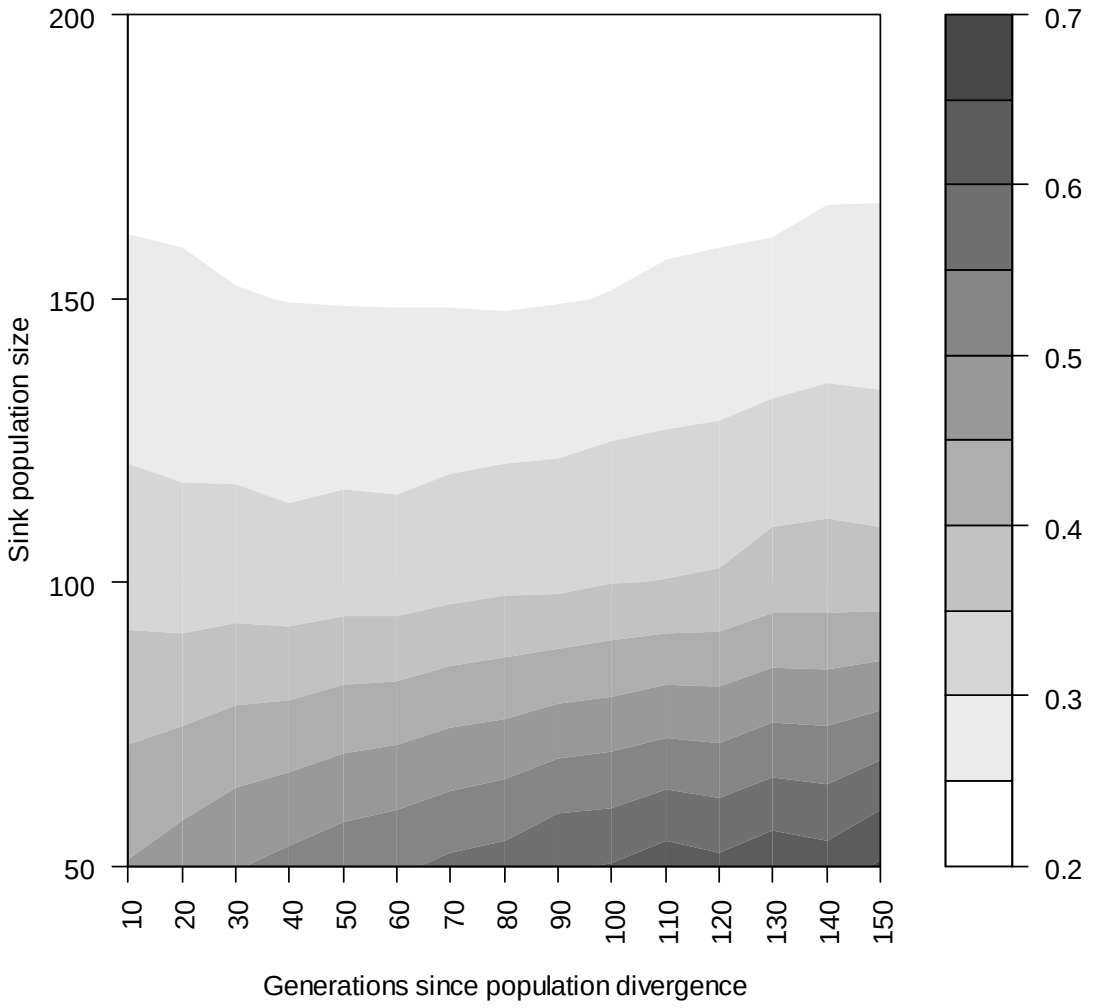


Figure 2.4. Contour plots of ongoing immigration rates required to produce a specific F_{ST} value between a simulated source and sink population, assuming different combinations of: 1) sink effective population size and 2) generations since the sink population split from the source population. The different shades represent different categories of immigration rates, with darker shades representing higher immigration rates. This figure is for an F_{ST} of 0.004, equivalent to the empirical value observed for Chinook salmon.

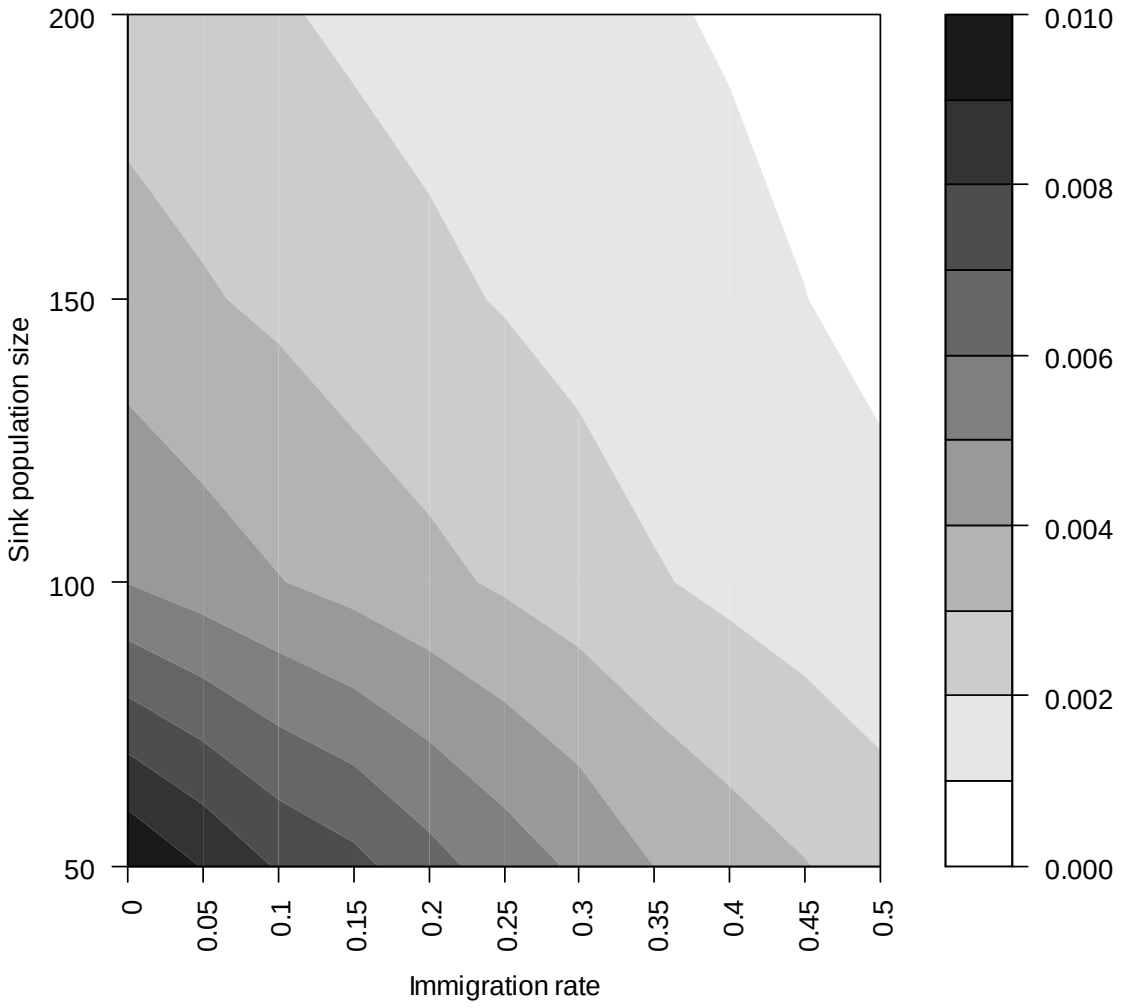


Figure 2.5. Contour plot of mean F_{ST} between a source and sink population after the populations have split and undergone one generation of reproduction and immigration, considering different combinations of sink population size and immigration rate. The different shades represent different categories of F_{ST} values, with darker shades denoting higher F_{ST} values.

Table 2.1. Summary of chum salmon samples with sample abbreviation, population collection site, date sampled, sample size (*N*), expected heterozygosity (H_{exp}) at 13 and 10 loci, and allelic richness (*AR*). Samples were collected from the Wood River (1-21), the Yukon River (22, 23) and the Nushagak river system counting towers (24-26). Allelic richness was calculated only for samples with $N \geq 10$.

#	Sample	Population	Date	N	Hexp (13 loci)	Hexp (10 loci)	AR (10 loci)
1	Joe04	Joe Creek	2004	3	0.53	0.55	
2	Pick04	Pick Creek	2004	9	0.67	0.62	
3	A05	A Creek	2005	1	0.46	0.50	
4	C05	C Creek	2005	1	0.27	0.35	
5	Elva05	Elva Creek	2005	18	0.71	0.65	6.46
6	Hid05	Hidden Lake Creek	2005	1	0.23	0.25	
7	Ice05	Ice Creek	2005	11	0.70	0.65	6.90
8	LTC05	Little Togiak Creek	2005	21	0.72	0.66	6.41
9	Lynx05	Lynx Creek	2005	3	0.48	0.49	
10	Pick05	Pick Creek	2005	1	0.23	0.25	
11	Bear06	Bear Creek	2006	4	0.57	0.56	
12	Elva06	Elva Creek	2006	7	0.69	0.65	
13	Fen06	Fenno Creek	2006	23	0.68	0.63	5.87
14	Hap06	Happy Creek	2006	6	0.64	0.59	
15	Ice06	Ice Creek	2006	42	0.73	0.67	6.32
16	LTC06	Little Togiak Creek	2006	14	0.70	0.66	6.40
17	Pick06	Pick Creek	2006	17	0.70	0.64	6.08
18	Sun06	Sunshine Creek	2006	46	0.72	0.66	6.21
19	WC06	Whitefish Creek	2006	2	0.56	0.53	
20	Wood06	Wood River	2006	10	0.67	0.60	6.17
21	Yako06	Yako Creek	2006	2	0.45	0.48	
22	AR04	Andreafsky River	2004	48	0.72	0.65	6.38
23	CR01	Chandalar River	2001	46	0.68	0.62	5.20
24	Nush04a	Nushagak River	2004 June 11	48	0.71	0.65	6.11
25	Nush04b	Nushagak River	2004 July 3	17	0.71	0.66	6.68
26	Nush04c	Nushagak River	2004 July 11	30	0.72	0.65	6.35

Table 2.2. Summary of Chinook salmon samples with sample abbreviation, population collection site, date sampled, sample size (*N*), expected heterozygosity (H_{exp}) at 12 and 11 loci, and allelic richness (*AR*). Samples were collected from the Wood River (1-6), the Yukon River (7, 8) and the Nushagak River system counting towers (9, 10). Allelic richness was calculated only for samples with $N \geq 10$.

#	Sample	Population	Date	N	H_{exp} (12 loci)	Hexp (11 loci)	AR (11 loci)
1	Elva04k	Elva Creek	2004	3	0.66	0.64	
2	Ice05k	Ice Creek	2005	3	0.68	0.67	
3	Elva06k	Elva Creek	2006	1	0.42	0.41	
4	Ice06k	Ice Creek	2006	27	0.74	0.73	9.87
5	LTR06k	Little Togiak River	2006	1	0.26	0.27	
6	Wood06k	Wood River	2006	6	0.72	0.71	
7	AR03k	Andreafsky River	2003	22	0.73	0.72	9.79
8	CR03k	Chandalar River	2003	30	0.69	0.67	8.23
9	Nush06ka	Nushagak River	2006 June	24	0.66	0.71	10.37
10	Nush06kb	Nushagak River	2006 July	24	0.67	0.75	9.92

Table 2.3. Genetic differentiation among chum salmon samples that had $N \geq 10$. Pairwise F_{ST} values are below the diagonal, and significant values after Bonferroni correction ($P < 0.05$) are marked with an asterisk. The numbers of loci that showed significant genotypic differentiation ($P < 0.05$, out of 10 loci) are above the diagonal.

	Elva05	Ice05	LTC05	Fen06	Ice06	LTC06	Pick06	Sun06	Wood06	AR04	CR01	Nush06b	Nush06c	Nush06a
Elva05		1	0	1	2	0	0	3	0	2	5	4	0	3
Ice05	0.0095		0	2	1	0	1	1	1	0	4	2	1	1
LTC05	0.0019	-0.0089		1	0	0	0	0	0	1	4	0	0	0
Fen06	0.0113*	0.0051	-0.0039		2	2	0	1	0	1	3	1	1	1
Ice06	0.0034*	0.0013	-0.0034	0.0052		1	0	1	0	1	4	1	0	1
LTC06	-0.0044	-0.0052	-0.0101	0.0056	0.0012		0	1	0	0	4	0	1	0
Pick06	0.0068	-0.0007	-0.0104	-0.0077	-0.0032	0.0006		0	0	0	3	0	1	0
Sun06	0.0094*	0.0009	-0.0001	-0.0014	0.0038	0.0071	-0.001		1	1	4	1	0	0
Wood06	-0.0013	-0.0017	-0.0077	-0.0084	-0.0046	0.0018	-0.01	-0.0035		0	5	0	0	0
AR04	0.0112*	-0.0058	-0.0034	0.0044	0.0034	-0.0003	-0.0018	0.0021	-0.0001		5	2	1	0
CR01	0.0393*	0.0220*	0.0204*	0.0234*	0.0246*	0.0217*	0.0129*	0.0263*	0.0260*	0.0238*		3	7	4
Nush06b	0.0077*	0.0006	-0.0068	-0.0021	-0.0028	-0.0008	-0.0057	0.0013	-0.0046	-0.0011	0.0200*		0	0
Nush06c	0.0003	0.0011	-0.0041	-0.0016	0.0014	0.0024	0.0013	-0.0031	-0.0094	0.0047	0.0474*	-0.0006		1
Nush06a	0.0133*	-0.0001	-0.0014	0.0000	0.0035	0.0093	-0.003	-0.0003	-0.0054	0.0012	0.0239*	0.0017	0.0026	

Table 2.4. Genetic differentiation among Chinook samples that had $N \geq 10$. Pairwise F_{ST} values are below the diagonal, and significant values after Bonferroni correction ($P < 0.05$) are marked with an asterisk. The numbers of loci that showed significant genotypic differentiation ($P < 0.05$, out of 11 loci) are above the diagonal.

	Ice06k	AR03k	CR03k	Nush06ak	Nush06bk
Ice06k	---	1	7	0	1
AR03k	0.0045	---	4	1	0
CR03k	0.0207*	0.0179*	---	5	6
Nush06ak	-0.0037	-0.0021	0.0161*	---	0
Nush06bk	0.0041	0.0021	0.0206*	-0.0007	---

Chapter 3: Selective effects of intense predation in wild populations of mature adult sockeye salmon

Abstract

Predation can be an important agent of natural selection in the wild, though empirical data on the evolutionary effects of predation are scant. Here, we quantified selection gradients in two populations of adult sockeye salmon (*Oncorhynchus nerka*) to determine whether bear predation selects for smaller body sizes and longer reproductive lifespans. Pedigrees were re-constructed for each population based on 11 microsatellite markers, and individual fitness was calculated as the number of returning adult offspring produced from a parental generation that was extensively sampled for the phenotypic traits of interest. Individual fitness was used to estimate selection coefficients and gradients for fish body length, standardized body depth, first date of stream entry, and reproductive lifespan. Selection differentials showed that reproductively successful parents in both populations had smaller bodies and longer in-stream lifespans, but selection coefficients indicated only stabilizing selection on body length in females and disruptive selection on lifespan for females from one population. There was also stabilizing selection on first date of stream entry in females and directional selection for later entry date in males from that population. Heritability estimates confirmed that all of these traits will potentially respond to selection. Thus, it appears that these populations do experience selective effects from predation but are also influenced by other types of

selection on body size, such as mate preference. These results show that interactions between different forms of selection may have substantial impacts on wild populations.

Introduction

Predation is an important agent of natural selection that can influence phenotypic divergence within species (Vamosi 2005), affecting life history, morphology and other traits (Nosil & Crespi 2006; Reznick & Endler 1982; Walker 1997). When predation pressure is high, selection favors adaptations that reduce predation risk and increase survival and opportunity for reproduction (Magnhagen 1991). For example, Trinidadian guppies (*Poecilia reticulata*) in high predation environments tend to be less colorful (Endler 1980) and mature earlier and reproduce more frequently than their counterparts in low predation environments (Reznick *et al.* 1996). By being less conspicuous and reproducing earlier and more often, individuals increase the probability of producing offspring before being killed. However, even in this extensively used evolutionary model system, there are few quantitative estimates of predation pressure and selectivity, which are critical for determining mechanistic links between predation and evolution in wild populations.

Pacific salmon (*Oncorhynchus* spp.) are another taxon where predation selection may have profound effects on life history and phenotypic traits. Salmon are subject to predation risk at multiple life stages. Juveniles are consumed by fish, avian, and mammalian predators in both freshwater and marine environments (Mayama & Ishida 2003; Olesiuk 1993), and these predators may selectively consume large individuals or be

gape-limited and so tend to consume smaller individuals. In addition, fisheries can remove large fractions of the population and be size-selective as well (Kendall *et al.* 2009). For semelparous adult salmon reaching the spawning grounds after surviving natural mortality and fisheries, bears can be a particularly important agent of predation selection (Quinn *et al.* 2003). Prior research indicates that bears preferentially kill large salmon (Quinn & Kinnison 1999; Reimchen 2000; Ruggerone *et al.* 2000), perhaps because large fish offer more food per capture effort, or because they are more noticeable and easier to catch, especially in smaller streams (Quinn 2005). Such size-selectivity likely contributes to morphological differences among stream populations (Quinn *et al.* 2001b).

Bear predation may also affect fitness by abbreviating an individual's reproductive lifespan (Quinn *et al.* 2001a). For example, bear predation may curtail reproductive activity by killing salmon that are not completely spawned out (Carlson *et al.* 2009), especially as there is a tendency for bears to kill salmon that have just arrived on the breeding area rather than post-spawning fish nearing death from senescence (Carlson *et al.* 2007). In addition to reduced opportunity to spawn, reproductive success may also be reduced by limiting redd (nest) defense in females (Hendry *et al.* 2004a). Thus when predation mortality is extremely high, traits that extend reproductive lifespan may be under strong selection. Adaptations to high predation may include evasive behavior (Klinka & Reimchen 2002) or rapid spawning after arrival at spawning streams, such that some reproduction occurs before an individual is killed (Gard 1971; Reimchen 2000).

Although selective effects of bear predation on salmon have been investigated previously (e.g. Carlson *et al.* 2007; Quinn & Kinnison 1999), selection has rarely been quantified in populations where predation potentially affects the vast majority of individuals. More importantly, the approaches to estimating predation selection have largely relied on indirect measures of individual fitness, such as: 1) size-specific probability of predation (Quinn & Kinnison 1999; Quinn & Buck 2001; Reimchen 2000; Ruggerone *et al.* 2000), 2) observations on survival of tagged fish (Quinn *et al.* 2001a), or 3) gonad depletion as a surrogate for reproductive success (Carlson *et al.* 2009). The more direct estimation of fitness, individual reproductive success from parent-offspring linkages (Howard 1979), has seldom been attempted, and past efforts were complicated by incomplete sampling (Dickerson *et al.* 2005).

Here, we quantified selection on two wild populations of sockeye salmon using individual reproductive success as the fitness measure. The populations spawn in geographically proximate streams, A and C creeks, in the Wood River Lakes system in southwestern Alaska (Fig. 3.1). Both populations experience heavy bear predation, but bears kill a higher fraction in A Creek and also kill the salmon earlier in their in-stream lives than in C Creek (Carlson *et al.* 2007). A Creek has little cover and a mean wetted depth of only 10 cm during the summer, so that bears can quickly kill most of the individuals in the stream at any given time. In contrast, C Creek is a slightly deeper stream (mean wetted depth of 14 cm) with cut banks where some fish can hide and avoid predation. These stream populations are good study systems because they are free from any hatchery influences or other anthropogenic source of habitat degradation or selection

in freshwater. They are subjected to commercial fishing at sea, but selection exerted by this fishery is well-documented (Kendall *et al.* 2009; Kendall & Quinn 2009). Thus, the effects of predation will reflect those found in natural habitat and may reveal fine-scale variation in selection patterns.

We have focused on the A and C creek populations because they experience intense predation, but it should be noted that the selection estimates will reflect all factors that affect offspring production, including sexual selection and fecundity. Sexual selection tends to favor larger individuals of both sexes (Blair *et al.* 1993; Quinn & Foote 1994), and larger females have higher fecundity (Manzer & Miki 1986). On the other hand, predation and stranding risk select against large, deep-bodied fish (Quinn *et al.* 2001a). These opposing selection pressures lead to the phenotypic diversity we observe in nature; in sockeye salmon, deeper streams often have deeper-bodied fish than shallower streams (Quinn *et al.* 2001b). Although interactions among these various selection pressures determine overall selection, we still expect that predation will have an especially strong influence on the A and C creek populations.

Our primary aim was to determine how high predation intensity contributes to natural selection in wild salmon populations. We hypothesized that factors relating directly to stream survival and hence reproductive opportunity would be under stronger selection in the stream with higher predation. Specifically, we expected that smaller body sizes, especially in males, and longer reproductive lifespans would be favored. To study selection in A and C creeks, we reconstructed one generation of parentage in each stream and quantified individual fitness as the number of returning adult offspring produced. We

used these fitness data to estimate selection measures on adult body length, body depth, spawn timing, and reproductive lifespan. By tagging fish individually and conducting daily stream surveys, we obtained detailed data on timing of predation events within streams, which we could then compare to the observed patterns of selection. For each population we also estimated heritabilities (h^2) of the traits evaluated for selection, to support predictions of potential evolutionary trajectories for these fish. Such parameters are more commonly estimated in hatchery than in wild populations (Carlson & Seamons 2008), making any estimates obtained for wild sockeye salmon of general interest.

Materials and methods

Sampling

A and C creeks are two small tributaries to Little Togiak Lake in the Wood River Lakes system in southwestern Alaska (Fig. 3.1). Several hundred mature sockeye salmon return to each stream every year, spawning from late July until late August. Sockeye salmon are the only species breeding in these streams, and there is no other proximate stream population within about 5 km, although there are several beach-spawning sockeye salmon populations within the lake. The streams are remote and relatively free of direct human impact, and brown bears (*Ursus arctos*) are the primary natural predators of the salmon. A Creek has approximately 0.37 km of spawning habitat accessible to fish, whereas C Creek has 0.44 km of available spawning habitat. To facilitate analysis of fish spatial distributions within the streams, each stream was divided into approximate 10 m

sections starting from the stream mouth, with a total of 31 sections in A Creek and 48 sections in C Creek.

Over 80% of the salmon in these streams return to spawn at age-4 (Quinn *et al.* 2001b), so the populations were sampled exhaustively during the summers of 2004 and 2008. Each year, the streams were monitored starting around July 20th, typically one week prior to entry of the first salmon. After fish started entering, the entire length of each stream was surveyed daily, and surveys continued until no live fish remained in the streams. During the surveys, all untagged individuals were captured and tagged, and the location of all tagged individuals was recorded. At each tagging event, the individual was measured, marked with a uniquely numbered plastic tag (see also Quinn *et al.* 2009; Quinn *et al.* 2001a), and sampled for fin tissue that was preserved in 95% ethanol. The dorso-ventral body depth from the anterior insertion of the dorsal fin to the belly and body length from the mid-eye to the end of the hypural bone were measured, comparable to other population-specific data from this and other systems (Quinn *et al.* 2001b). Standardized body depths were calculated following Ihssen (1981), to obtain a measure of body depth corrected for body length. When tagged individuals were encountered, we recorded the first stream section where the fish was observed. During about 50% of the surveys, the reproductive status of individual females was determined by handling each fish and squeezing her gently to observe whether she were ready to spawn, and if so, whether she still had eggs or had spawned completely. The number of days to complete spawning out was calculated as the days elapsed between the first day of stream entry and the day an individual was categorized as being spawned out. Males were assumed ready

to spawn at all times because they always released milt when squeezed. When a salmon carcass was found, the tag, stream section, and mode of death (killed by a bear or senescent) were recorded. Fin clips were taken from untagged carcasses for genetic analysis, and if the body was intact, measurements of body length and depth were taken as well. Although body depths are not directly comparable between ripe and spawned out fish, the body measurements of carcasses were still used for analysis, as we had no other morphological data for these untagged individuals. All carcasses were removed from the stream to prevent resampling. Otoliths were collected from a subset (~25%) of both the tagged and untagged carcasses for age determination. Overall sampling coverage was excellent since both A and C creeks have mean wetted stream depths less than 20 cm, making fish easy to observe and capture.

The tag observations provided empirical data for several factors potentially affecting survival and reproductive success of individual fish. For each individual, we calculated first date of stream entry (which was assumed to relate to initiation of reproductive opportunity) and two measures relating to reproductive lifespan, defined as the time between the stream entry and senescence (Hendry *et al.* 2004a). The first measure was called 'in-stream lifespan' and was calculated as the number of days between stream entry and last day an individual was seen alive, plus one day so that the minimum lifespan was one day. The second measure was called 'days observed' and was calculated as the number of days a fish was actually observed alive in the stream. We included this second measure because some individuals left the stream for the lake and subsequently re-entered the stream. Daily female to male sex ratios were also estimated for live fish. A

and C creeks are separated by < 2 km (Fig. 3.1), and some individuals were observed in both streams. We initially assumed that an individual spawned in the stream where it was observed more frequently, and fish that were observed with the same frequency in both streams had no specific spawning location designated. However, if an individual with an ambiguous spawning location was later determined to have produced offspring that returned to C Creek, for example, that individual was then designated as belonging to the C Creek population. These retrospective population assignments were applied to eight females and 20 males, and in all cases the new assignment was to the C Creek population. To examine temporal variation in bear predation, daily predation indices were calculated as the number of bear-killed fish divided by the total number of fish (live, bear-killed, and senescent) counted that day.

ANOVA was also used to compare mean phenotypic trait values between A and C creek fish of each sex. Population attributes that were based on counts, including sex ratios and proportions of carcasses killed by bears, were compared between streams using Chi-square tests. Mann-Whitney-Wilcoxon tests were used to determine trait differences between bear-killed and senescent individuals, as sample variances were highly unequal. We also tested for linear correlations between phenotypic traits, within streams and sexes.

Genetic analysis

Parentage was determined using 11 highly polymorphic microsatellite markers: *One100, One102, One103, One106, One108, One109, One111, One112, One114, One115* (Olsen *et al.* 2000), *One110c* (J. Seeb, pers. comm., F: 5'-

GAGTGGCCGTCGTTTTACCCTCCATTTCAATCTCATCC-3' and R: 5'-GCGCATGGTCATAGCTGTTACAGAGAACAGTGAGGGAGC -3'), and *Ots103* (Beacham *et al.* 1998). DNA was extracted from fin tissue using kits (QIAGEN , Valencia, CA, USA) and standard protocols, and markers were amplified via polymerase chain reaction (PCR).

The QIAGEN Multiplex PCR kit was used to amplify the microsatellite markers in three panels. Panel 1 included *One100*, *One103*, *One106*, *One110c*, and *Ots103*; Panel 2 included *One109*, *One111*, *One112*, and *One114*; Panel 3 included *One102*, *One108*, and *One115*. Multiplex PCRs were set up for each panel, with each PCR consisting of 2µl extracted DNA, 1x QIAGEN Multiplex PCR Master Mix, 0.2µM of each primer, and water to make up a total 10µl reaction volume. For panels 1 and 2, each reaction underwent an initial polymerase activation and DNA denaturation at 95°C (15 min), followed by 31 cycles of denaturation at 94°C (30 s), annealing at 58.5°C (90 s), and extension at 72°C (60 s). Finally, the reactions were held at 60°C (30 min) and then at 4°C (5 min). Panel 3 reactions followed the same protocol except that the annealing temperature was 60°C.

All forward primers were labeled with fluorescent dye, and the labeled PCR fragments were size-separated on a MegaBACE 1000 (Amersham Biosciences) sequencer and run with an appropriate size standard. Allele fragment size estimates were obtained using Genetic Profiler genotyping software (Amersham Biosciences). Genotyping error rates were quantified by re-genotyping a subset of 64 individual DNA extractions, chosen at random from both the 2004 and 2008 samples. Discrepancies

between the original genotype and the genotype obtained from the re-run were considered errors from sample mishandling or scoring, and error rates were estimated using PEDANT (Johnson & Haydon 2007).

The microsatellite data were tested for deviations from Hardy-Weinberg and linkage equilibrium using GENEPOP version 4.0.10 (Raymond & Rousset 1995). MICROCHECKER (van Oosterhout *et al.* 2004) was used to check for evidence of stuttering, large allele dropout, and null alleles. The program CERVUS 3.0 (Kalinowski *et al.* 2007) was used to calculate locus-specific exclusion probabilities for parentage assignment.

Pedigree reconstruction

Data for potential parents (adults in 2004) and offspring (adults in 2008) were used in COLONY (Jones & Wang 2010) to determine parentage via maximum likelihood. COLONY infers parentage and sibships jointly using the likelihood of the full pedigree, a more efficient and accurate approach than comparing likelihoods of individual pairwise relationships (Walling *et al.* 2010). COLONY also accounts for different genotyping error rates among markers. Data from both streams were analyzed together to increase candidate parent and offspring pools and to check for offspring that strayed between streams (i.e., spawned in a stream other than where their parents spawned). Because only candidate parents from 2004 and candidate offspring from 2008 were analyzed, we lacked samples for candidate parents of three or five year old offspring sampled in 2008 as well as any three or five year old offspring of 2004 candidate parents. Nevertheless,

93% of individuals in both streams were age-4 (Table 3.1) so the missing groups of samples were likely small.

Fifteen candidate parents that lacked sex information were included in both candidate mother and father files. The probability of sampling the true parent was conservatively set to 0.5 for both mothers and fathers, even though actual sampling probabilities were likely higher than 50%. Genotyping error rates were set to the error rates estimated from genotyping re-runs. COLONY outputs maternal and paternal assignments along with probability estimates, and only assignments with probabilities of 0.95 or higher were accepted, following Hauser et al. (2011).

Selection analysis

Selection analyses were performed separately on the two populations because we were primarily interested in comparing selection between them. Reproductive success (RS) was the fitness metric for selection analyses, defined as the number of returning adult offspring per spawner. The opportunity for selection I was calculated as I = variance(RS)/mean(RS)^2 and can be considered the upper limit on the strength of selection (Arnold & Wade 1984; Brodie *et al.* 1995). Non-standardized selection differentials were calculated as the trait mean for selected adults (parents that produced at least one returning adult offspring) minus the trait mean for all adults (Lande 1980), and these were used to calculate responses to selection. Standardized selection differentials, which are calculated as the non-standardized selection differential divided by the standard deviation of the trait, were also estimated to obtain a measure of total selection

on each trait, including both direct selection and indirect selection on correlated traits (Kingsolver *et al.* 2001).

Linear (β) and quadratic (γ) selection gradients were estimated using multiple linear regressions of standardized phenotypic trait values against relative fitness, following Lande and Arnold (1983). Relative fitness was calculated as individual reproductive success divided by mean reproductive success within each sex. To avoid statistical complications arising from multicollinearity (Graham 2003), traits that were strongly correlated ($r^2 > 0.20$; see Table 2 for correlations) were not included together within a regression model. We estimated selection gradients for two sets of traits: 1) absolute body depth, date of first entry, and reproductive lifespan, and 2) body length, standardized body depth, date of first entry, and reproductive lifespan. We used these two trait sets because we were interested in selection on both absolute and standardized body depths. Since body length is highly correlated with absolute but not standardized body depth (Table 3.2), it could be included in the regressions that used standardized body depth. In-stream lifespan and the number of days observed in the stream were tested separately as the measure of reproductive lifespan within each set of traits. Death fate (bear-killed versus senescent) was not included because bears transported 22-44% carcasses before we had the opportunity to observe them (Quinn *et al.* 2009). Thus, many individuals did not have a death fate, and including that factor in the model would substantially reduce sample sizes.

Trait values were standardized to a mean of zero and standard deviation of one for use in the regressions. Two types of multiple regressions were applied to each dataset:

one regression including all traits to estimate linear selection gradients, and a second regression including all traits, their squared terms, and their cross products to estimate non-linear selection gradients. Linear selection gradients indicate directional selection, quadratic selection gradients indicate stabilizing or disruptive selection, and interaction (correlational) coefficients represent selection on combinations of traits.

Selection gradients are often estimated using ordinary least squares (OLS) regression (e.g. Anderson *et al.* 2010), but OLS regressions assume that the dependent data are normally distributed and that the independent variables are measured without error. Likelihood-ratio tests indicated that the individual fitness data used here were zero-inflated and over-dispersed for both sexes in both streams ($P < 0.001$), since many individuals produced no returning adult offspring. Thus, two types of regressions were used. First, we performed OLS regressions to obtain coefficients that could be directly interpreted and facilitate comparison of our results with those from other studies. Second, we performed zero-inflated negative binomial (ZINB) regressions because they were expected to better fit the over-dispersed, zero-inflated data (Zuur *et al.* 2009). ZINB regressions essentially consist of two steps: in the first step, the probability of obtaining a zero value is modeled with a binomial error distribution and logit link function. This information is then used in the second step, which models counts using a negative binomial generalized linear model and log link function (Zuur *et al.* 2009). Model fits were compared using the Akaike information criterion (AIC). AIC values corrected for sample size (AIC_C; Hurvich & Tsai 1993) were also estimated, but we used the uncorrected AIC values because the two estimators produced nearly identical results.

The regression coefficients obtained from OLS regressions can be considered equivalent to the linear selection gradients (Lande & Arnold 1983), whereas quadratic selection gradients are calculated as double the quadratic selection coefficients (Stinchcombe *et al.* 2008). We compared our selection gradients to gradients estimated in other wild populations (Siepielski *et al.* 2009) to assess the relative strength of selection in the A and C creek populations. The ZINB regression coefficients are in logarithmic space due to the log link and are not directly comparable to selection gradients estimated by OLS, but they could still be used to determine modes of selection (directional, stabilizing, or quadratic).

Univariate cubic spline analysis (Schluter 1988), a nonparametric technique that makes no assumptions about the functional form of the selection surface, was used to visualize the relationships between phenotypic traits (body length, absolute and standardized body depth, first day of stream entry, lifespan, and days observed) and fitness. Predicted relationships between fitness and phenotypic trait values were created using generalized additive models (GAM function in R, mgcv package), assuming a negative binomial error structure and estimating the dispersion parameter Θ as $\text{mean}(RS)^2 / [\text{var}(RS) - \text{mean}(RS)]$ (Hilborn & Mangel 1997). For each spline, a smoothing factor λ of 0.03 was used.

Estimating heritabilities

According to the univariate breeder's equation, the evolutionary response resulting from selection acting on a quantitative trait is described $R = h^2S$, where R is the response, h^2 is the narrow-sense heritability of the trait, and S is the selection differential

(Lynch & Walsh 1998). Narrow sense heritability (h^2) equals V_A/V_P, where V_A is additive genetic variance, and V_P is total phenotypic variance. Narrow sense heritability therefore indicates the proportion of total phenotypic variance in a trait due to additive genetic effects.

Heritabilities were calculated separately for the two streams because heritability is considered a population-specific parameter (Visscher *et al.* 2008). Heritabilities were estimated for adult body length, absolute and standardized body depth, lifespan, days observed, and stream entry date. First, we obtained estimates of sex-specific heritabilities using parent-offspring regression (daughters on mother, daughters on fathers, sons on mothers, sons on fathers), adjusting the estimates by the ratios of standard deviations within each sex (Falconer & McKay 1996). We then estimated heritabilities using the MCMCglmm package in R (Hadfield 2010). MCMCglmm analyzes data in a Bayesian framework and can estimate variance components using the animal model, which analyzes data on all relationships simultaneously and is sufficiently flexible to cope with missing data and unbalanced sampling designs (Wilson *et al.* 2010). More specifically, the animal model uses the breeding value of each individual, as estimated from the phenotypes of its relatives, as a random factor to estimate genetic variances and heritabilities of analyzed traits.

Multiple priors were tested, and we settled on the weakly informative priors recommended in Wilson et al. (2010), because they provided reasonable heritability estimates comparable to the ones obtained from the parent-offspring regressions. Specifically, priors were generated by partitioning phenotypic variance equally into

genetic and residual components, and little weight was placed on the values specified in the prior. Each chain was run with a 50,000 iteration burn-in followed by 200,000 iterations, and sampling took place every 100 iterations. Posterior densities and traces were used to check for convergence. Sex was modeled as a fixed effect and mother as a random effect because deviance information criterion (DIC) indicated that these factors explained substantial proportions of variances in each trait. The sex-specific heritabilities estimated using parent-offspring regression were compared with the estimates from MCMCglmm.

Results

Basic data comparisons between and within streams

Salmon from A and C creeks differed in some phenotypic traits in the 2004 parental generation. Based on ANOVA with sex as a fixed effect, mean body length, absolute and standardized body depth, lifespan, and number of days observed were greater in C Creek than in A Creek (Table 3.1; $F = 9.0$, $P = 0.002$ for length; $F = 13.1$, $P < 0.001$ for absolute depth; $F = 17.0$, $P < 0.001$ for standardized depth, $F = 418.0$, $P < 0.001$ for lifespan; $F = 420.1$, $P < 0.001$ for days observed). However, a chi-square test showed that age structure did not differ significantly between streams, with most fish being age-4 ($X^2=3.1$, $P = 0.08$; Table 3.1). The mean date of first stream entry was 5 days later in A Creek (Table 3.1; $F = 200.6$, $P < 0.001$), and A Creek individuals were observed more frequently within the streams during their in-stream lifespans (0.88 in A Creek versus 0.79 in C Creek; Table 3.1; $F = 66.4$, $P < 0.001$).

Some phenotypic traits were correlated within streams and sexes. Body length and absolute body depth were positively correlated, and larger individuals entered the streams earlier (Tables 3.2, 3.3). Additionally, individuals that left the stream (proportion of days observed in the stream < 1) had longer total in-stream lifespans than fish that were seen in the creek every day (Tables 3.2, 3.3). C Creek females that entered the stream earlier had longer reproductive lifespans than females that entered later, and C Creek males with shallower standardized body depths had longer in-stream lifespans than males with larger standardized body depths, but no other groups showed these relationships (Table 3.3). The lifespan estimates used in these comparisons were for all fish, including those that died from predation and of senescence.

The two streams showed distinct distributions of sockeye salmon over space and time. In A Creek, salmon densities within each stream section fluctuated over the spawning season. The highest densities initially occurred in the uppermost 100 m of the stream, but toward the end of the season, fish were found mostly in the lower 200 m (Fig. 3.2). There also appeared to be four distinct periods of high overall density, each lasting for a few days as salmon entered and were subsequently killed or died of senescence (Fig. 3.2). C Creek had higher and more stable salmon densities overall than those in A Creek. There was some spatial separation within the C Creek (Fig. 3.3), with salmon spawning above and below a beaver dam which broke on August 8, 2004.

Females outnumbered males two to one in both streams (Table 3.1), but sex ratios did not differ between streams ($X^2 = 2.0$, $P = 0.15$). In both streams, sex ratios became more female-biased as the spawning season progressed (Fig. 3.4). A larger proportion of

females reached spawned-out status in C Creek (30.7%) than in A Creek (20.1%) presumably due to higher predation in A Creek, but the difference was not significant (X^2=0.66, P = 0. 42). Data on female reproductive status indicated that females started spawning shortly after stream entry, as ripe individuals typically became partially-spawned or spawned out within several days (Fig. 3.5). The mean number of days for females to become spawned out did not differ significantly between streams (5.0 days in C Creek versus 3.9 days in A Creek; F = 2.30, P = 0.13).

Various measures indicated that both the A and C creek populations experienced intense bear predation. A Creek had a significantly higher proportion of carcasses that were bear-killed (as opposed to senescent: 99% vs. 74% in C Creek, X^2 = 114.3, P < 0.001). However, mean daily predation intensity did not differ significantly between streams (paired t-test t = 1.45, P = 0. 16; Figs. 3.6 and 3.7). These measures of predation were conservative because bears removed an estimated 22% of individuals in A Creek and 44% of individuals in C Creek over the course of the spawning season (Quinn *et al.* 2009), and data from transported individuals were not included when estimating predation.

The predation indices were also used to determine whether spatial and temporal components should be included in the selection gradient models. Broad spatial and temporal divisions were designated within each stream based on where and when live fish appeared to cluster, as predation rates are density-dependent (Quinn *et al.* 2003). A Creek had four spatial divisions, and C Creek had three (Figs. 3.2, 3.3). According to ANOVA tests, the spatial divisions did not differ significantly in daily predation intensity

in either A Creek ($F = 0.13$, $P = 0.94$) or C Creek ($F = 1.0$, $P = 0.37$), and thus spawning location was not included in the regression models used to estimate selection gradients. However, the temporal divisions (Figs. 3.2, 3.3) differed in predation intensity ($F = 8.9$, $P < 0.001$ in A Creek; $F = 8.0$, $P < 0.001$ in C Creek), and thus date of first stream entry was included in the regressions. Tukey tests showed that predation was significantly lower on the latest spawners in A Creek ($P = 0.01$ or less in pairwise comparisons with the other temporal divisions), and predation was lowest in the second wave of spawners in C Creek ($P = 0.01$ or less in pairwise comparisons with the other temporal divisions). Mean predation indices for each division are listed in the supplementary table 3.S3.

Bear-killed and senescent fish differed primarily in traits related to reproductive lifespan (Table 3.4). Bear-killed males in both streams had significantly higher proportions of days observed in the stream (W = 208, $P = 0.05$ for A Creek; W = 1100.5, $P = 0.03$ for C Creek), but females did not (Table 3.4). In C Creek, bear-killed individuals had a significantly shorter mean in-stream lifespan (W = 2766.5, $P < 0.001$ for females; W = 338.5, $P < 0.001$ for males) and were observed on fewer days in the stream (W = 2618.5, $P < 0.001$ for females; W = 323, $P < 0.001$ for males) than senescent individuals (Table 3.4). In A Creek, bear-killed and senescent males did not differ in mean in-stream lifespan, but bear-killed females were observed in the stream on fewer days than senescent females (W = 306.5, $P = 0.05$; Table 3). The lack of a lifespan difference in A Creek males was probably due to sample sizes, as only two senescent males were found. There were no significant spawn timing and morphological differences between bear-killed and senescent fish, except that senescent A Creek males were shorter

and had shallower standardized body depths than bear-killed males ($P = 0.018$ for body length, $P = 0.039$ for standardized body depth).

Genetic analysis

Estimated genotyping error rates were low, with mean allele dropout error rate of 0.006 and a mean false allele error rate of 0.017 (Hauser *et al.* 2011). GENEPOP indicated that 5 of 11 loci were significantly out of Hardy-Weinberg equilibrium in the 2004 A Creek fish (One100, One102, One106, One111, One115), and the 2008 A Creek fish (One100, One102, One103, One106, One115; Table 3.S1). In C Creek, 10 of 11 loci were out of Hardy-Weinberg equilibrium in both 2004 (One110c was the exception) and 2008 (One111 was the exception; Table 3.S2). F_{IS} values were generally small in magnitude (<0.05) except those for One100, One106, and One115 (Table 3.S1). GENEPOP also found very high levels of linkage disequilibrium: of 55 pairwise comparisons between loci, 100% in A Creek 2004, 98% in C Creek 2004, 85% in A Creek 2008, and 92% in C Creek 2008 were significantly out of equilibrium ($P < 0.05$). MICROCHECKER found no indication of stuttering or large allele dropout. Genetic variation was sufficiently high for the purpose of parentage assignment; per locus, the mean number of alleles was 18.3, the mean proportion of individuals genotyped was 0.95, and mean expected heterozygosity was 0.85. CERVUS estimated that the combined exclusion probability was 0.9999 for a single parent and greater than 0.9999 for two parents.

Pedigree reconstruction

Across both the A and C creek populations, 80% of offspring had at least one parent assigned (Table 3.5): 62% of the offspring had both parents assigned with at least 0.95 probability for each parent, 14% of the remaining offspring had only the mother assigned, and 4% had only the father assigned. A total of 159 mating pairs were identified, where both the mother and father were sampled. The phenotypic data proved useful for corroborating the plausibility of genetic parentage assignments. Only two of the mating pairs had a mother and father that were not observed in the same stream, and 10 pairs consisted of parents that were not observed in the creek during overlapping time periods. Another test of assignment plausibility was to check if any of the 3- or 5-year old offspring, for which candidate parents should not have been sampled, had parents assigned with high probability ($P \geq 0.95$). One of two age-3 offspring and three of 59 age-5 offspring were assigned both a mother and a father. In addition, five age-5 offspring had a single parent assigned.

Reproductive success varied substantially among individuals (Fig. 3.8). Most candidate parents produced no returning adult offspring (85% for A Creek females, 73% for A Creek males, 83% for C Creek females, and 78% for C Creek males). The fish with the highest individual reproductive success within each stream were both males; one A Creek male produced 14 adult offspring, and one C Creek male produced 29 adult offspring. Within each stream, females had lower mean reproductive success than males because there were twice as many females as males (Table 3.1). The only stream-sex grouping with mean reproductive success greater than one was C Creek males (Table

3.1), but the 2004 populations were about half the size of the 2008 populations in both streams, supporting the observation of high variance in reproductive success. Bear-killed and senescent individuals did not differ in the number of returning adult offspring produced, but interestingly, bear-killed females produced fewer offspring relative than senescent females, whereas bear-killed males produced more offspring than senescent males (Table 3.4).

Selection analysis

The opportunity for selection (*I*) was higher for females than for males in both streams (Table 3.1), likely because there were more than twice as many females as males, resulting in lower mean reproductive success in females as compared to males. Selection differentials were negative for body length, body depth, and proportion of days observed in the stream, and positive for date of first entry into the stream and in-stream lifespan (Tables 3.6 and 3.7). In other words, parents that successfully produced returning adult offspring had smaller bodies and longer in-stream lifespans, entered the streams later during the spawning season, and were not observed as consistently during the stream surveys. The selection differentials for days observed were also positive except in C Creek females.

Several regression models for estimating selection coefficients were tested, and we used AIC values and direct comparisons of results to select a model. Zero-inflated regressions always fit the data better than OLS regressions, but the measure of reproductive lifespan (in-stream lifespan or days observed) and the set of traits included in the regression did not strongly affect AIC (Tables 3.8 and 3.9). Regression coefficients

were similar for body length and absolute body depth, so we focused on the trait set including body length, standardized body depth, first day of stream entry, and reproductive lifespan. We then chose days observed as the measure of reproductive lifespan, because in-stream lifespan and days observed showed similar selection patterns, but regressions using days observed had a higher number of significant selection coefficients. Thus, the results described below are for a zero-inflated model with body length, standardized body depth, first day of stream entry, and days observed as the predictors.

The selection coefficients revealed a variety of selection patterns across sexes and streams. The only significant directional selection coefficient was for later day of first stream entry in A Creek males (Table 3.10), but a greater number of significant non-linear selection coefficients were detected (Table 3.11). In A Creek females, there was stabilizing selection on body length and stream entry date, and disruptive selection on lifespan. They also showed a negative interaction between body length and standardized body depth, suggesting that females with long but relatively shallow bodies had higher reproductive success. In A Creek males, there was stabilizing selection on body depth, but interaction coefficients suggested that the fitness of males with relatively shallow body depths increased with lifespan. For C Creek females, there was stabilizing selection on body length, standardized body depth, and stream entry date. Interaction coefficients suggested that longer individuals with shallower standardized body depths had higher fitness, as did later entering individuals that entered later but were observed for fewer days in the stream. No significant selection coefficients were detected for C Creek males,

likely due to low sample size. In fact, regressions for C Creek males sometimes failed to converge (Table 3.11).

The univariate cubic splines offered a visual depiction of selection patterns that were generally consistent with those inferred from the selection coefficients. The splines suggested stabilizing or minimal selection on morphological traits, with slightly larger body sizes favored for both sexes in C Creek (Figs. 3.9, 3.10, 3.11). Individuals that entered the stream later were favored in A Creek, whereas fish arriving towards the middle of spawning season had high fitness in C Creek (Fig. 3.12). The cubic splines for in-stream lifespan indicated stabilizing selection on females in both streams and positive directional selection on males (Fig. 3.13). As for number of days observed, patterns differed between streams, with apparent directional selection for a greater number of days in A Creek, disruptive selection on C Creek females, and stabilizing selection on C Creek males (Fig. 3.14). The splines associated with in-stream lifespan and days observed were the least consistent with the selection patterns indicated by the selection coefficients.

Estimating heritabilities and responses to selection

The heritabilities estimated using parent-offspring regression varied more than the heritabilities estimated using MCMCglmm, but both methods indicated high heritability for day of first stream entry (Tables 3.12 and 3. 13). We will focus on the MCMCglmm estimates here, because they are based on more data than the parent-offspring regression estimates and should therefore be more accurate. The heritability estimates ranged from 0.11 to 0.61 (Table 3.13), values that were comparable to those obtained for other salmonid populations (Carlson and Seamons 2008). Heritability values were similar

between streams for morphological traits and reproductive lifespan, but A Creek had substantially higher heritability for date of first stream entry. Responses to selection were calculated using the estimated heritabilities (Table 3.13) and selection differentials (Table 3.6), based on the univariate breeder's equation. The results indicated that all traits would respond to selection and result in smaller bodies, longer reproductive lifespans, and earlier date of stream entry, with date of stream entry showing the greatest potential response (Table 3.14). The 2008 adult data (offspring of 2004 adults) suggested that fish morphological traits did not respond as expected, since the salmon were slightly larger in 2008 (Table 3.1). However, both date of first stream entry and reproductive lifespan did show the expected evolutionary response, with salmon entering the streams later in the season and having longer reproductive lifespans.

Discussion

Both the A and C creek sockeye salmon populations sustained heavy levels of predation that likely affected the observed selection patterns. We expected that smaller body sizes and longer reproductive lifespans might be favored in these stream populations, and indeed, selection differentials showed that successful parents at both sites had smaller bodies and lived longer in the streams. However, few significant directional selection coefficients were detected; stabilizing selection on body length was observed in females from both streams as well as A Creek males, and disruptive selection on lifespan was observed in A Creek females. There was also indication of selection on stream entry date, which was stabilizing in females and directional favoring later entry in A Creek males. Some combinations of traits appeared to be under negative correlational

selection. Longer but relatively shallow bodied females in both streams had higher fitness, and smaller-bodied males in A Creek had higher fitness when they had longer reproductive lifespans (in terms of days observed). Heritability values were also estimated for all traits, and the potential responses to selection appeared especially high for day of first stream entry, consistent with controlled breeding experiments with salmon (e.g. Quinn *et al.* 2011; Quinn *et al.* 2000) and field estimates using parentage analysis (Dickerson *et al.* 2005).

These results suggested that although smaller body sizes and longer reproductive lifespans contribute to individual fitness, there may not be strong and consistent directional selection on these phenotypic traits even in populations that are subject to high predation. Indeed, the stabilizing selection on body length suggested that there may be antagonistic interactions between different types of selection on morphological traits. Even if predation favors small body sizes, for instance, sexual selection for larger body sizes and increased fecundity may counteract the survival-based selection (Quinn *et al.* 2001a). Some of the correlational selection coefficients showed how selection might be antagonistic. For example, there was a negative interaction between body length and standardized body depth in females. Longer females may have been more fecund and sexually attractive to males, but having relatively shallow body depths may have also improved fitness for these larger individuals by reducing predation risk and improving mobility in the stream habitat. In another example, smaller A Creek males had higher reproductive success when they had longer reproductive lifespans. Thus, even if smaller

males are less attractive sexually, they may still spawn successfully by staying alive longer.

Longer reproductive lifespans may increase individual fitness in several ways, and thus it was somewhat surprising that direct selection for longer lifespans was not detected. Longer-lived females have increased opportunity to defend against redd superimposition by other females (Hendry *et al.* 2004a; McPhee & Quinn 1998), and longer-lived males may have more mating opportunities (Fleming 1998). However, when all individuals have a very high risk of being killed by bears, as is the case in both A and C creeks, there may be strong impetus to spawn immediately upon stream entry. Previous research has shown that bear predation can select for faster senescence in salmon, and A Creek fish in particular senesce earlier than C Creek fish and other populations in the Wood River system (Carlson *et al.* 2007). Indeed, the pedigree data showed that even individuals with lifespans as short as one day successfully produced returning adult offspring.

One caveat may be that although males can reproduce quickly, females typically require several days to construct redds and spawn all their eggs (McPhee & Quinn 1998). However, a previous study suggests that females in high predation environments can complete spawning only two days after constructing their redds (Clark 1959), a finding supported by the data collected in this study on reproductive status of females (Fig. 3.5). Additionally, A and C creeks often have high salmon densities (Figs. 3.2, 3.3), such that redd sites are limited. There were some field observations that after a female was killed, a new female moved in and started guarding the previously-constructed redd, so that the

new female could start spawning fairly quickly. Indeed, the estimated selection on reproductive lifespan, particularly the disruptive selection observed for A Creek females, suggested that individuals may employ different spawning strategies. Some salmon may spawn quickly and have reproductive success despite an abbreviated lifespan, whereas others may derive a fitness advantage from living longer. For instance, long-lived females may can guard their redds from superimposition by other females, although there may be variation in efficacy of redd guarding. Previous work on a population of pink salmon (*O. gorbuscha*) subject to bear predation found a positive correlation between lifespan and reproductive success in males, but not in females, perhaps because females could guard their redds for 30% of the run at most (Dickerson *et al.* 2005). In A and C creeks, opportunities to guard redds and mate multiple times may be especially variable due to the high predation risk.

Spawn timing may affect individual fitness due to its relationships with various biotic and abiotic factors. For example, fish that attempt to spawn when bear activity is high are more likely to suffer mortality and may have reduced reproductive opportunities (Carlson *et al.* 2009). Later stream entry was favored in A Creek males, perhaps because those males arrived during a window of relatively low predation later in the season (see Fig. 3.6, around Aug 20). Alternatively, later arriving males may have had higher fitness because male to female ratios decreased over the spawning season (Fig. 3.4), potentially increasing mating opportunities for those males. In C Creek females, there was a negative interaction between selection on body length and entry date (Table 3.11), suggesting that small-bodied fish were favored toward the end of the spawning season. One possible

explanation is that larger females were better able to construct redds early in the season, but at the end of the season, females simply took over previously constructed redd sites and did not have to expend as much energy to spawn, increasing the fitness of small-bodied females.

Other agents of selection operate on these populations as well, notably harvest selection. Fishery exploitation rates and selectivity for different body sizes in Wood River sockeye salmon have varied over time, but interestingly, populations with small-bodied fish sometimes experience greater harvest selectivity for smaller body sizes than populations with larger fish (Kendall & Quinn 2009); the difference in harvest vulnerability between larger and smaller fish within each population is more pronounced in the populations with smaller fish overall. Thus, it appears likely that the fishery may contribute to selection against larger body size in the A and C creek populations, which consist of relatively small fish. The biased sex ratios in these streams (Fig. 3.4) support this idea, as males are typically larger-bodied and are often more heavily exploited by the fishery than females (Kendall & Quinn 2009). Harvest selection seems less likely to affect date of first stream entry and reproductive lifespan, unless those traits are strongly correlated with body size, because date of migration through the fishery is only weakly related to spawning date (Doctor *et al.* 2010).

Parentage assignment rates were fairly high considering that these populations are not closed, and we were confident in assignment accuracy. Most fathers and mothers were observed in the same stream at the same time, even though data from both populations were run together for parentage assignment. In addition, the parentage

assignments in A Creek were confirmed using a set of 80 SNP (single nucleotide polymorphism) loci (Hauser *et al.* 2011). There were some assignment errors based on the ages of the individuals, but some of those ages may have been inaccurate due to mistakes in otolith reads (Neilson 1992).

The selection gradients estimated for A and C creeks were generally comparable to those estimated in other natural populations. One exception was the directional selection gradient on stream date for A Creek males (0.78; Table 3.10), which exceeded the 90th percentile of linear selection gradients in a database compiled by Siepielski et al. (2009). The quadratic selection gradients (γ values) for body length (-0.42 for A Creek females, -0.62 for A Creek males, -0.34 for C Creek females; Table 3.11) had magnitudes between the 60th and 80th percentiles of quadratic selection gradients in the database, even after applying the following correction to the database gradients. Many γ values in the database may have been erroneously estimated as non-linear regression coefficients, when the actual gradient should be the coefficient multiplied by two (Stinchcombe *et al.* 2008). Hence, we multiplied all quadratic coefficients in the database by two before calculating percentiles, which will tend to overestimate the coefficients and make our comparison conservative. The selection gradients estimated for this study were also comparable in magnitude to those estimated for other Pacific salmon species (Anderson *et al.* 2010; Ford *et al.* 2008; Seamons *et al.* 2007).

Heritability estimates were greater than zero for all of the traits analyzed, indicating the potential for evolutionary responses in these traits. The sample sizes were probably somewhat modest for estimating heritabilities with high precision, but the

estimates obtained from this study are still useful, as there are few published heritabilities for sockeye salmon and for wild salmonid populations in particular (Carlson & Seamons 2008). Our results also corroborate experimental studies that have demonstrated a genetic component to migration and spawn timing in salmon (Dickerson *et al.* 2005; Quinn *et al.* 2011; Quinn *et al.* 2000). The estimated responses to selection (Table 3.14), suggested that selection favors smaller bodies, longer reproductive lifespans, and later stream entry, but based on the phenotypes of the adults sampled in 2008, the expected responses were observed only for reproductive lifespan and date of stream entry. Mean body length and body depth were slightly larger in 2008 than in 2004 (Table 3.1), potentially suggesting that selection is not temporally stable. Indeed, most of the significant selection gradients detected in this study were non-linear, supporting the idea that the A and C creek populations do not experience consistent directional selection over time. Selection varies spatiotemporally in many real-world populations (Bell 2010), including those of salmonids (Seamons *et al.* 2007), and there is no reason to expect that the A and C creek populations are exceptions. Analyzing additional years of data would certainly contribute to a more complete picture of selection on these salmon; for example, the intensity of bear predation varies among years (unpublished data) and may cause variation of selection gradients as well. Additional years of data are currently being analyzed and will be presented in future research.

In conclusion, this study demonstrated that intense bear predation may favor smaller body sizes and longer reproductive lifespans in A and C creek sockeye salmon. Thus, predation has likely contributed to the evolution of small body sizes in these

populations, even though predation selection almost certainly interacts with other selective pressures such as sexual and harvest selection. These various types of selection shape the intraspecific diversity we observe in nature, and it would therefore be prudent to consider the effects of selection in the management of these wild populations.

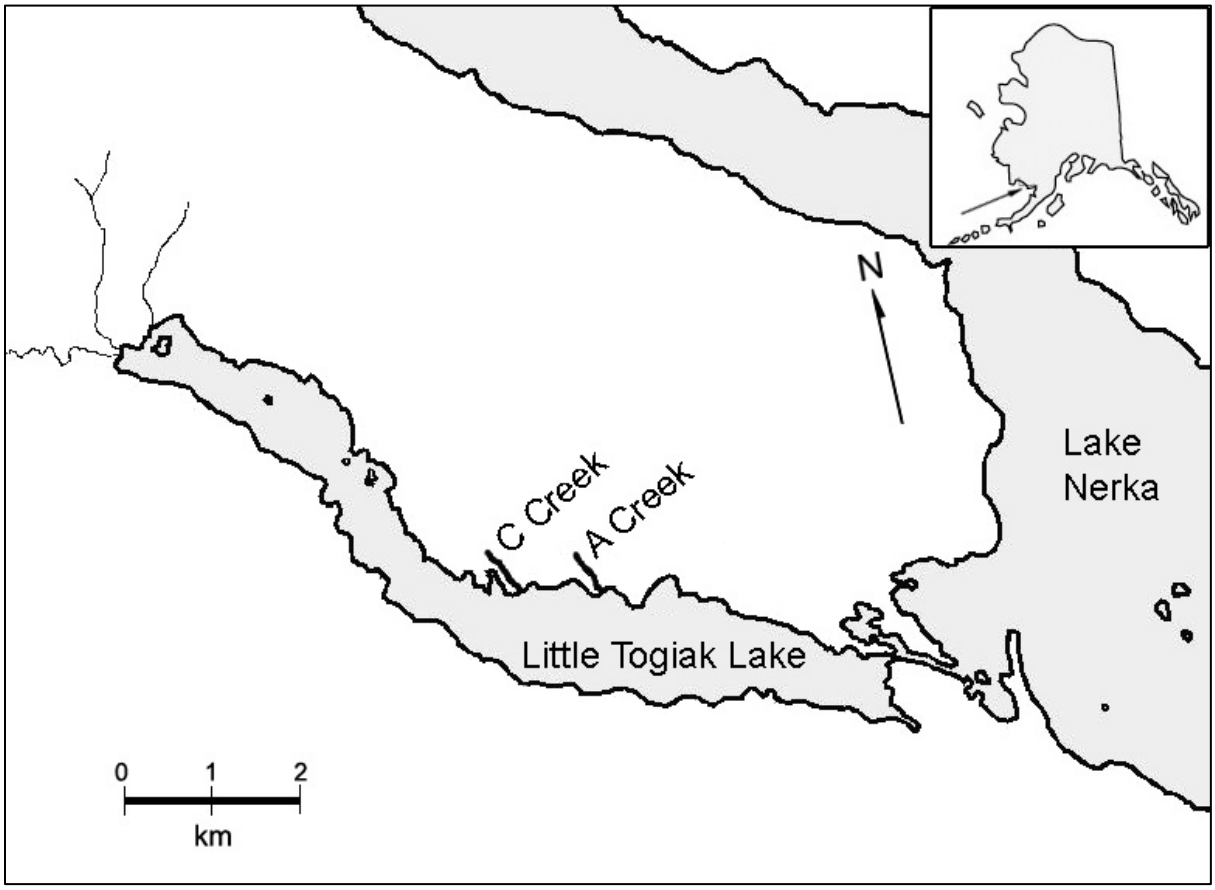


Figure 3.1. Map of the study sites (A Creek and C Creek) in southwestern Alaska.

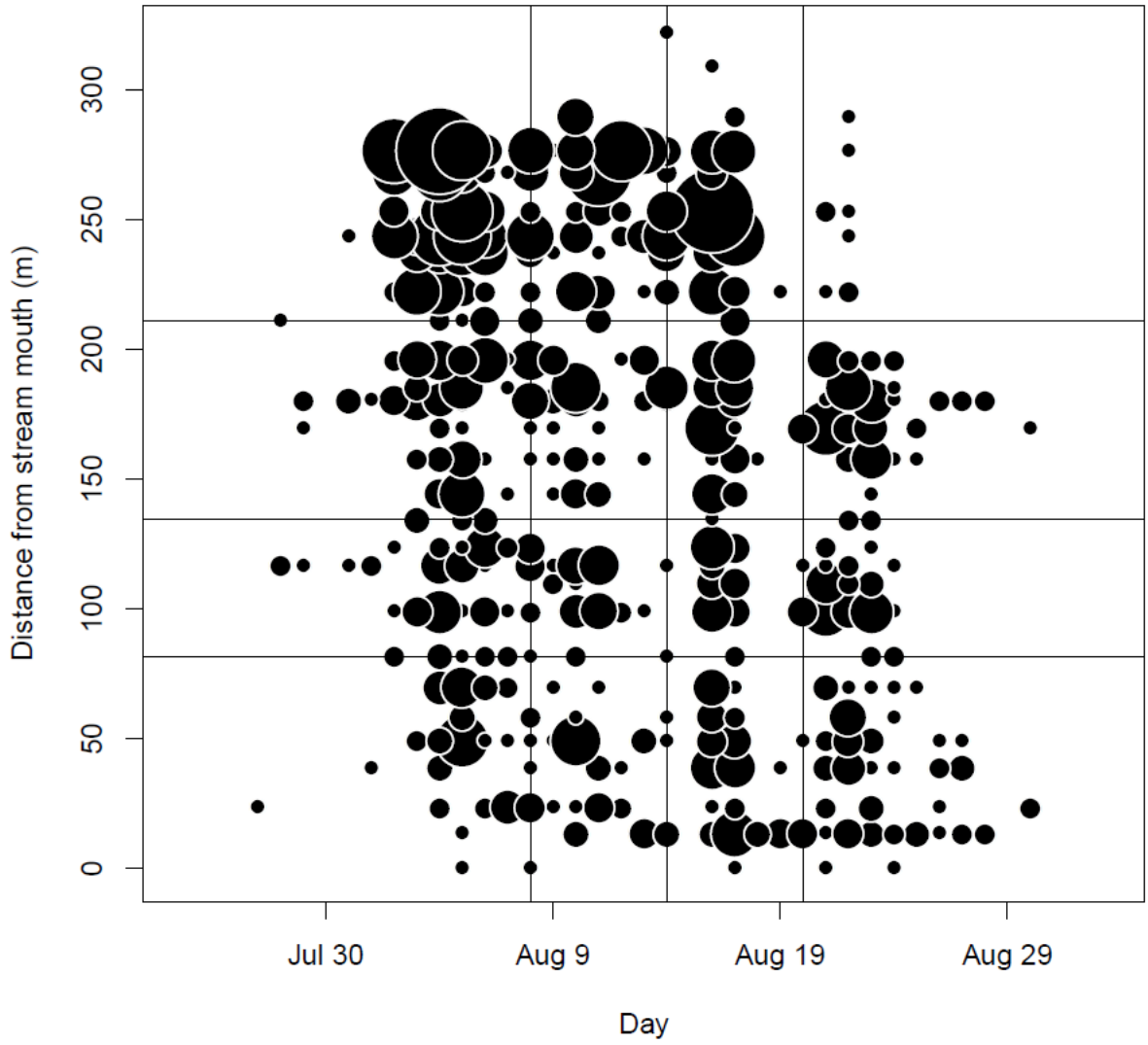


Figure 3.2. Stream locations of individuals in A Creek during the 2004 spawning season, with circle sizes corresponding to the number of fish observed at that location. Horizontal lines represent spatial divisions, and vertical lines represent temporal divisions, both defined by where and when fish clustered.

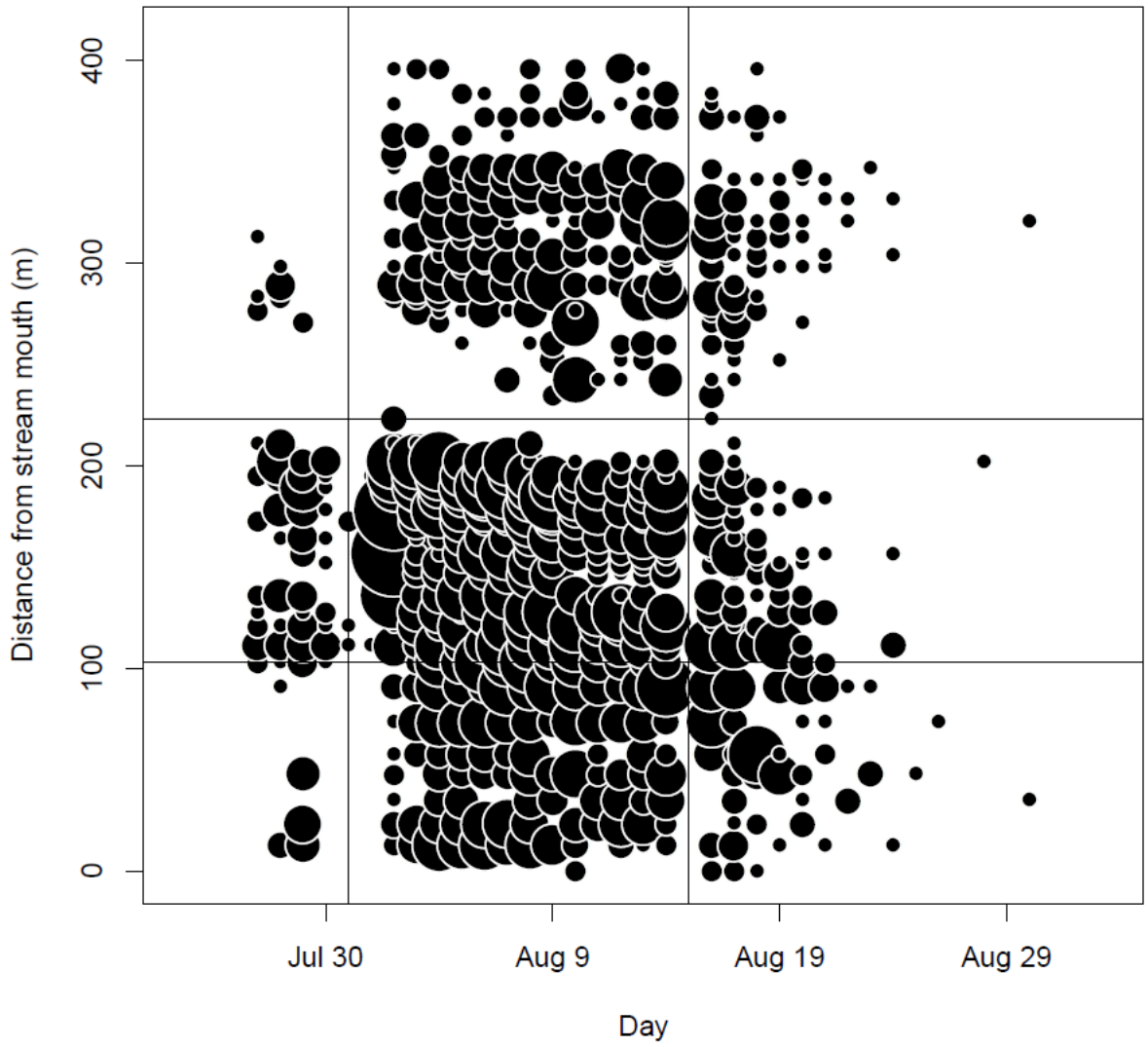


Figure 3.3. Stream locations of individuals in A Creek during the 2004 spawning season, with circle sizes corresponding to the number of fish observed at that location. Horizontal lines represent spatial divisions, and vertical lines represent temporal divisions, both defined by where and when fish clustered.

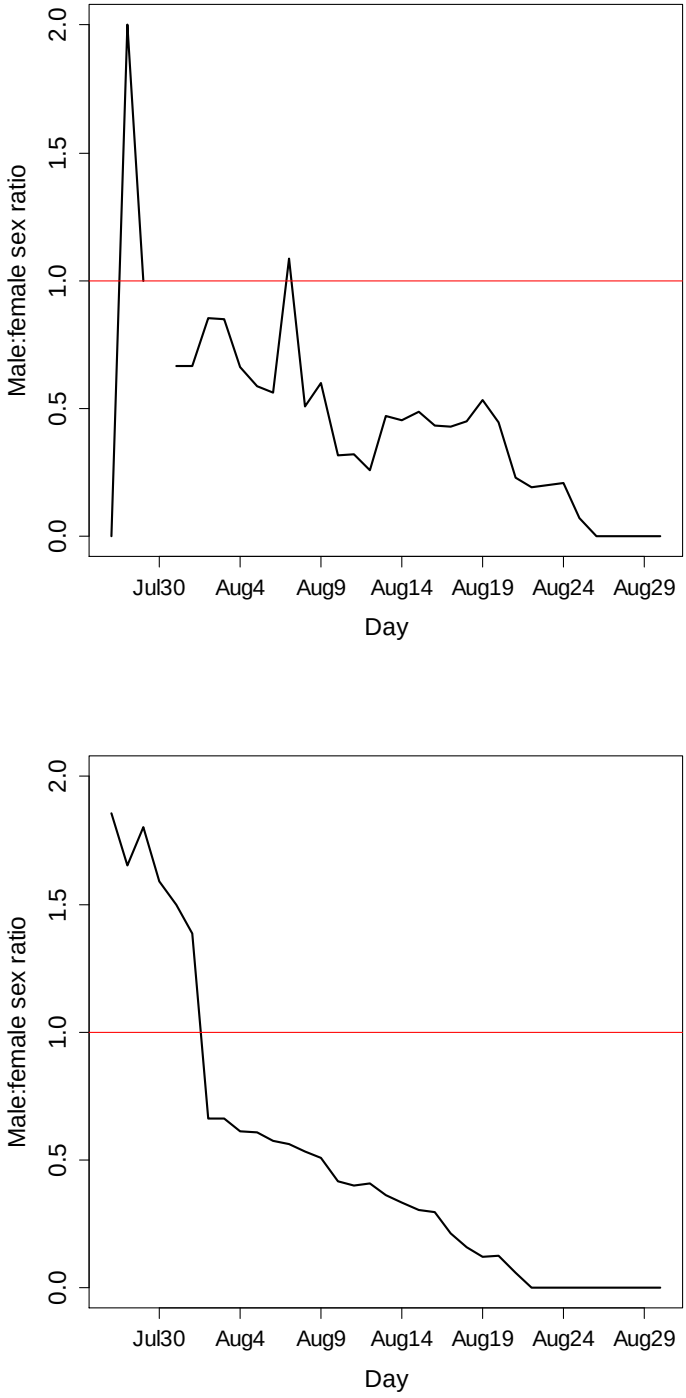


Figure 3.4. Male to female sex ratios over the course of the spawning season in 2004, with the red line denoting a 1:1 sex ratio. Data for A Creek are on the top, and data for C Creek are on the bottom. The break in the A Creek figure occurred because no fish were observed that day.

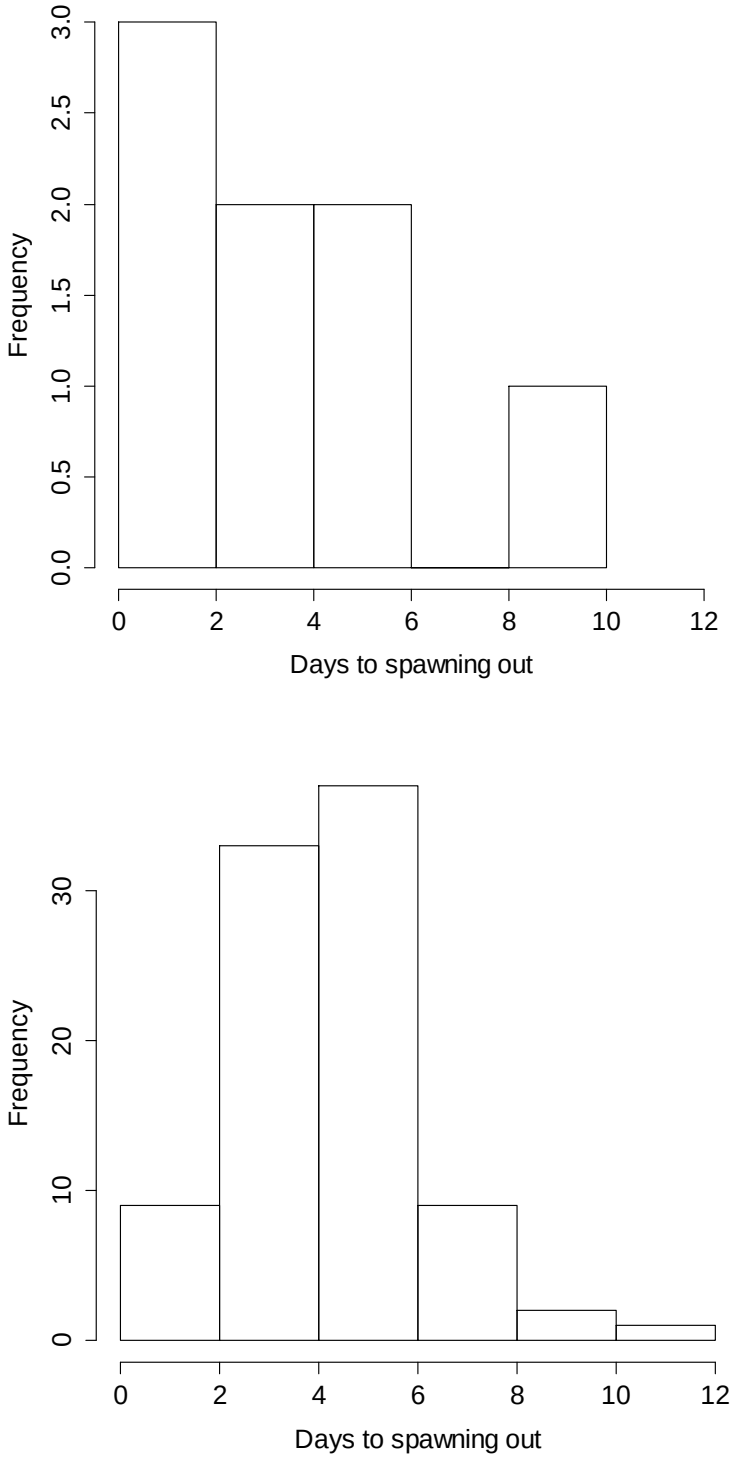


Figure 3.5. Frequency histograms of the number of days until spawning out for females in A Creek (top) and C Creek (bottom) in 2004.

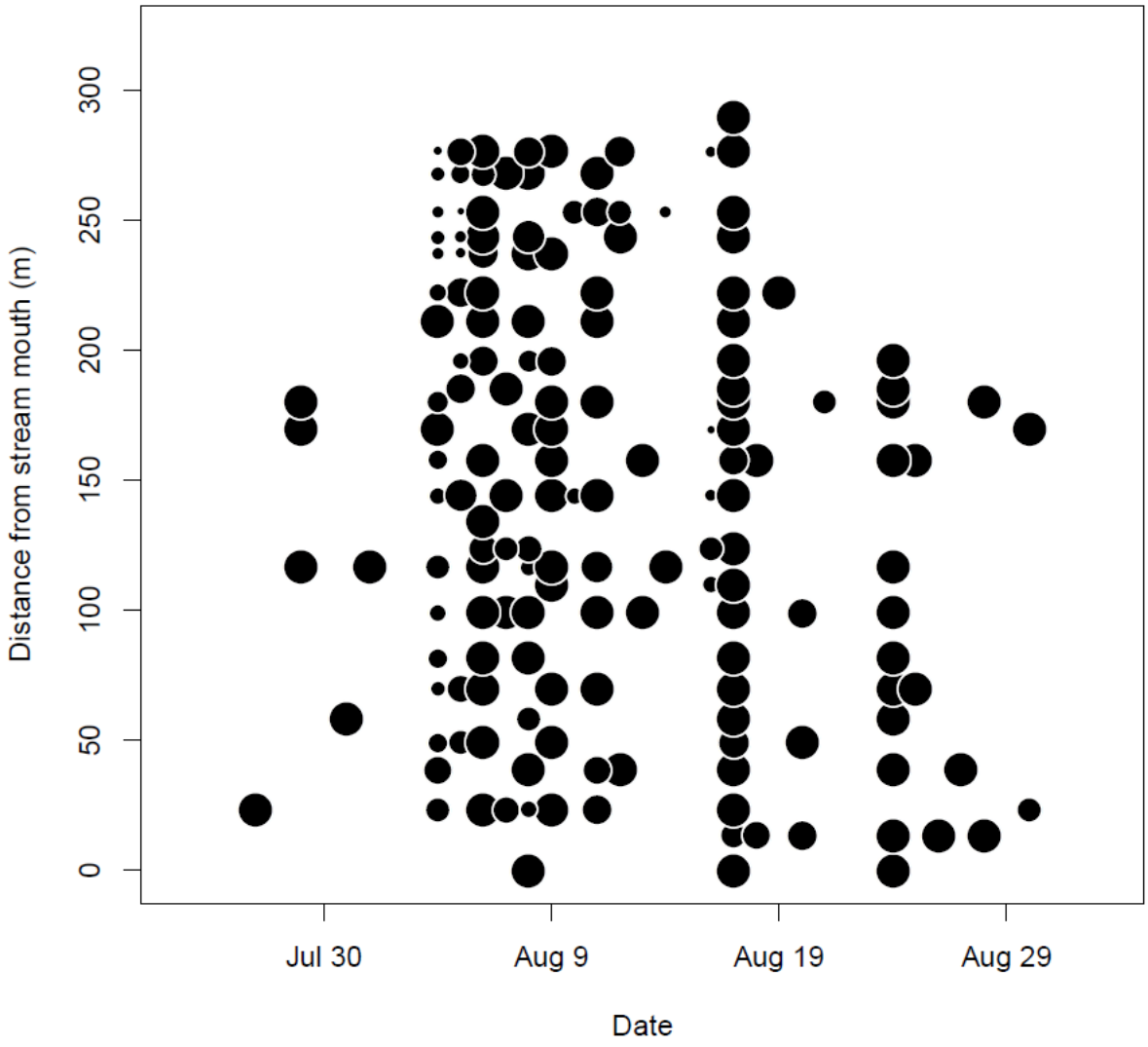


Figure 3.6. Location-specific bubble plot of predation indices throughout the 2004 spawning season in A Creek. Circle sizes are proportional to the predation index, which varied from 0 to 1.

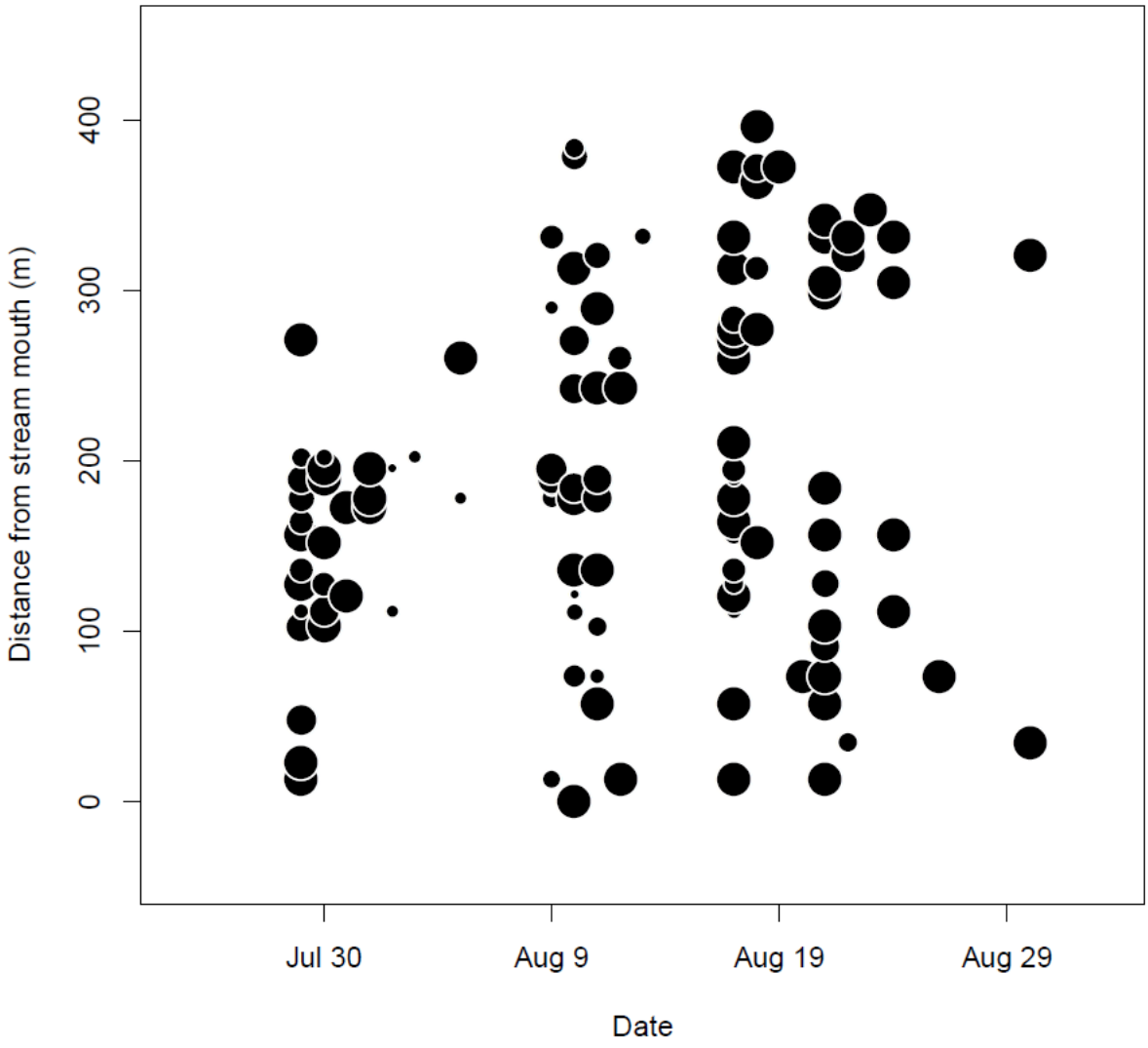


Figure 3.7. Location-specific bubble plot of predation indices throughout the 2004 spawning season in C Creek. Circle sizes are proportional to the predation index, which varied from 0 to 1.

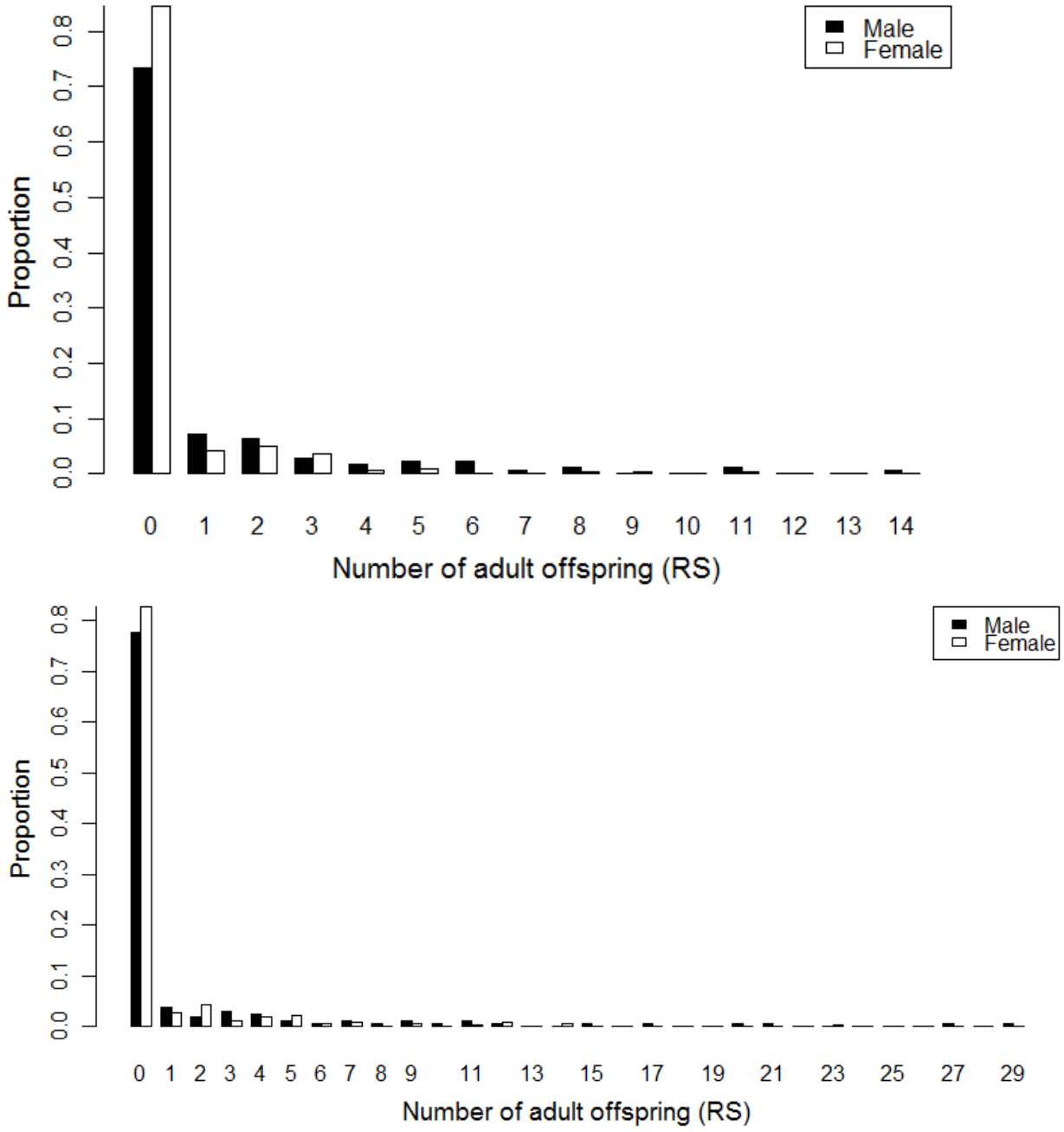


Figure 3.8. Frequency histograms of number of adult offspring produced per potential parent in A Creek (top) and C Creek (bottom), separated by males and females.

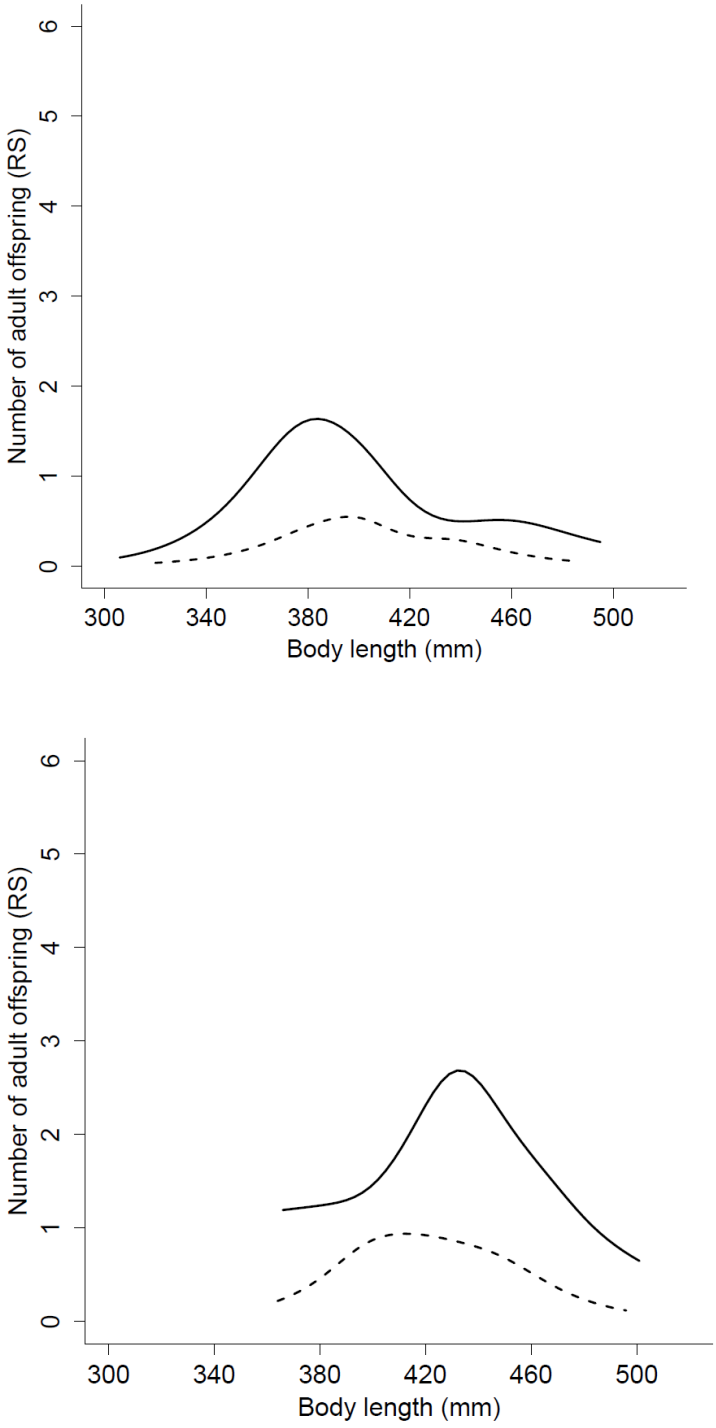


Figure 3.9. Cubic splines describing the relationship between body length and reproductive success, for female (solid line) and male (dashed line) candidate parents sampled in 2004. The A Creek splines are on top, and C Creek splines are on the bottom.

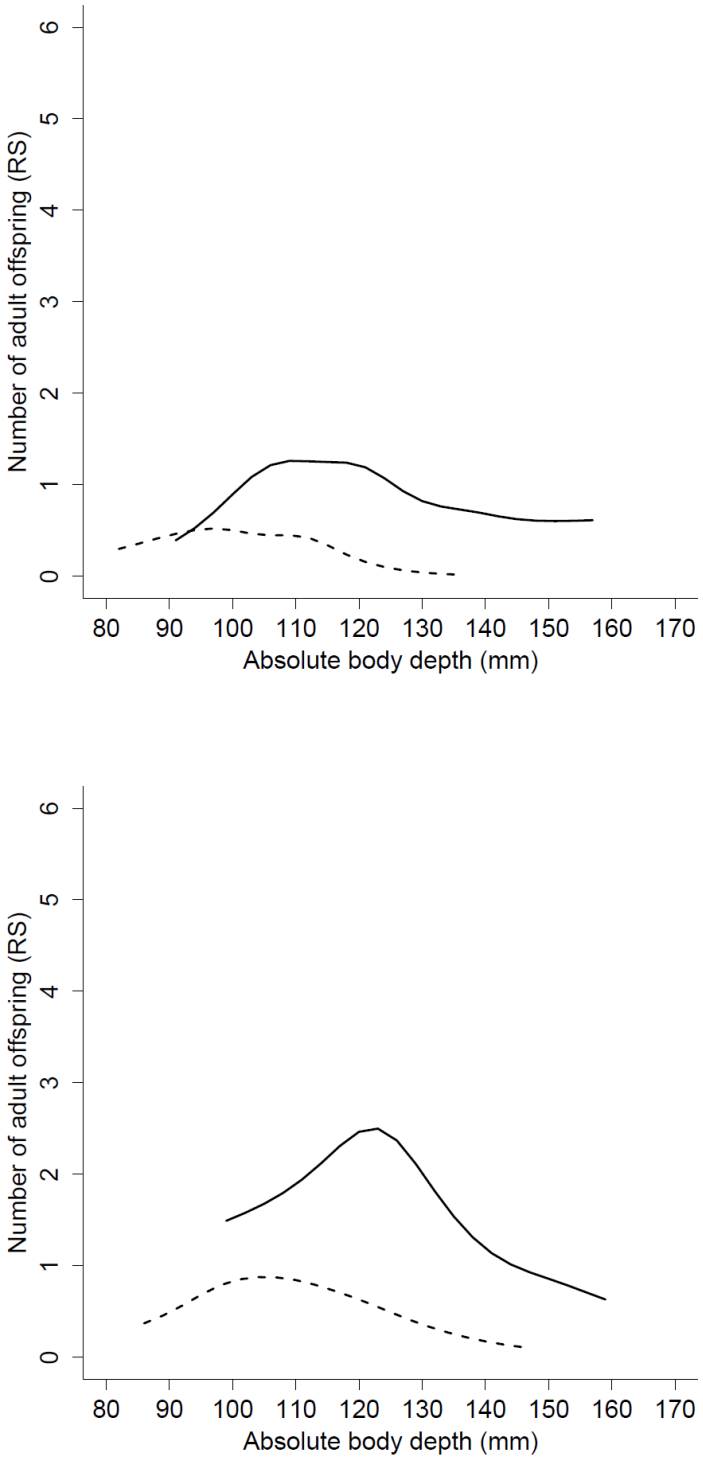


Figure 3.10. Cubic splines describing the relationship between absolute body depth and reproductive success, for female (solid line) and male (dashed line) candidate parents sampled in 2004. The A Creek splines are on top, and C Creek splines are on the bottom.

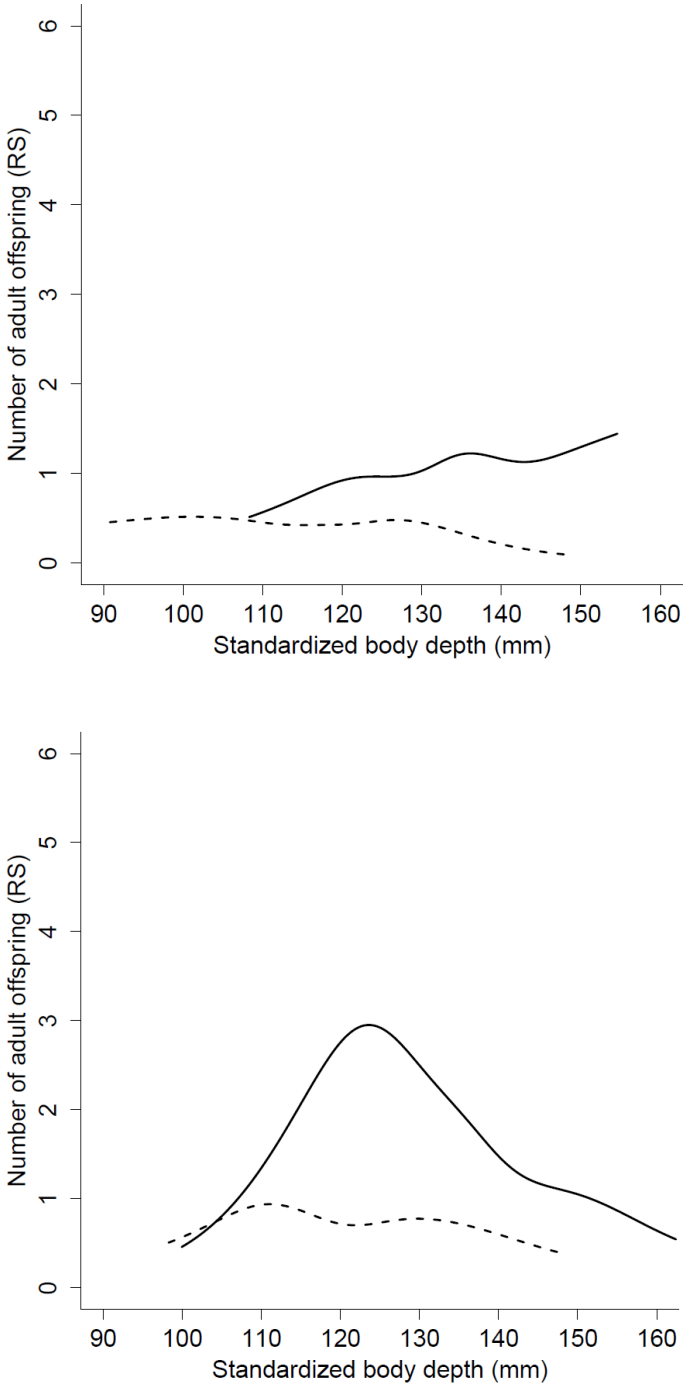


Figure 3.11. Cubic splines describing the relationship between standardized body depth and reproductive success, for female (solid line) and male (dashed line) candidate parents sampled in 2004. The A Creek splines are on top, and C Creek splines are on the bottom.

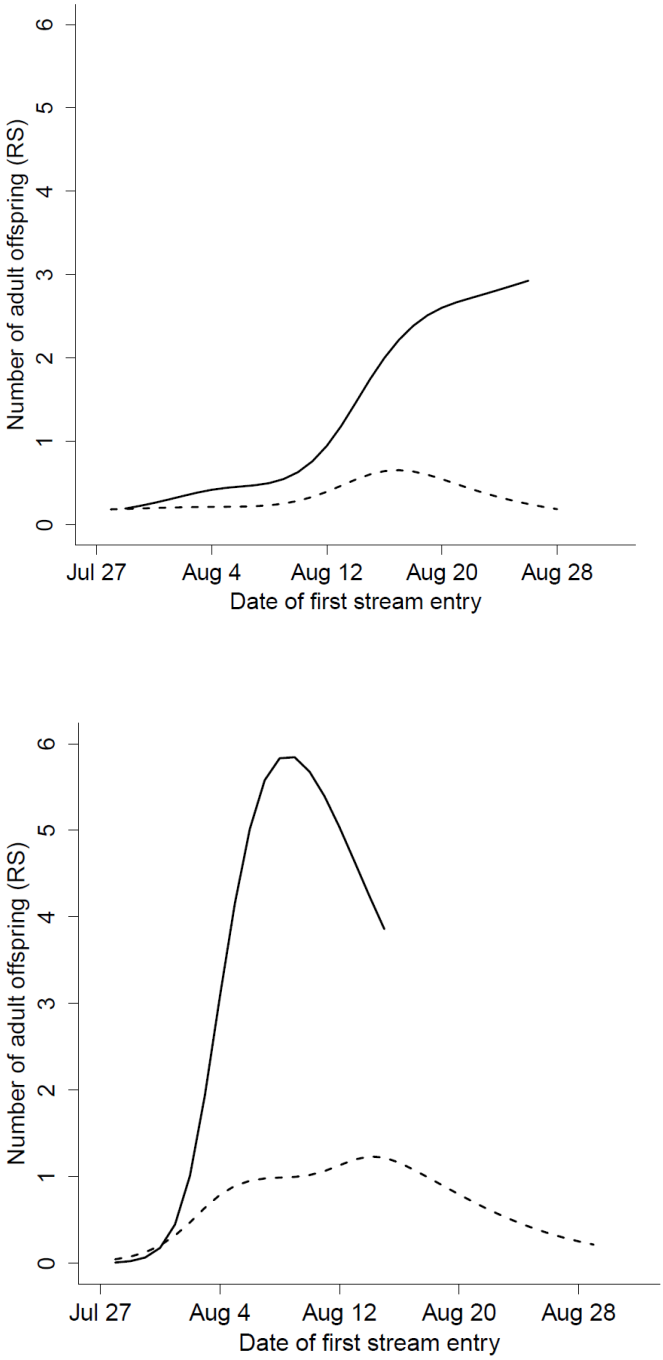


Figure 3.12. Cubic splines describing the relationship between date of first entry into the creek and reproductive success, for female (solid line) and male (dashed line) candidate parents sampled in 2004. The A Creek splines are on top, and C Creek splines are on the bottom.

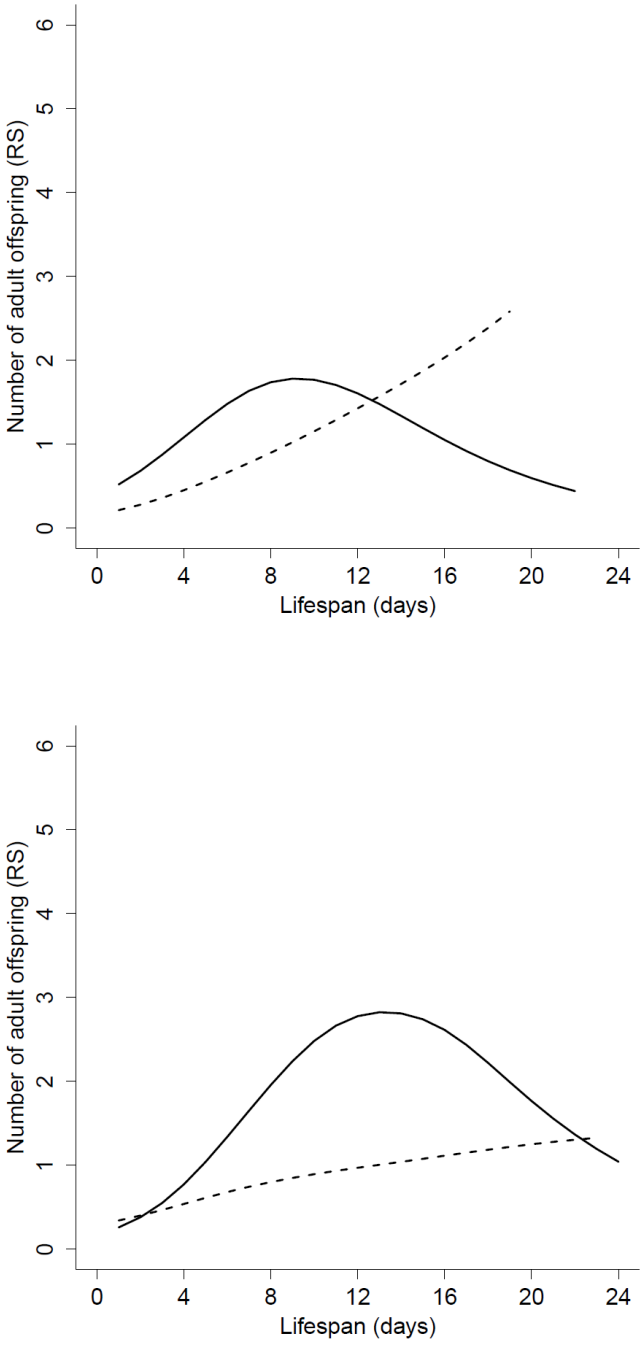


Figure 3.13. Cubic splines describing the relationship between in-stream lifespan and reproductive success, for female (solid line) and male (dashed line) candidate parents sampled in 2004. The A Creek splines are on top, and C Creek splines are on the bottom.

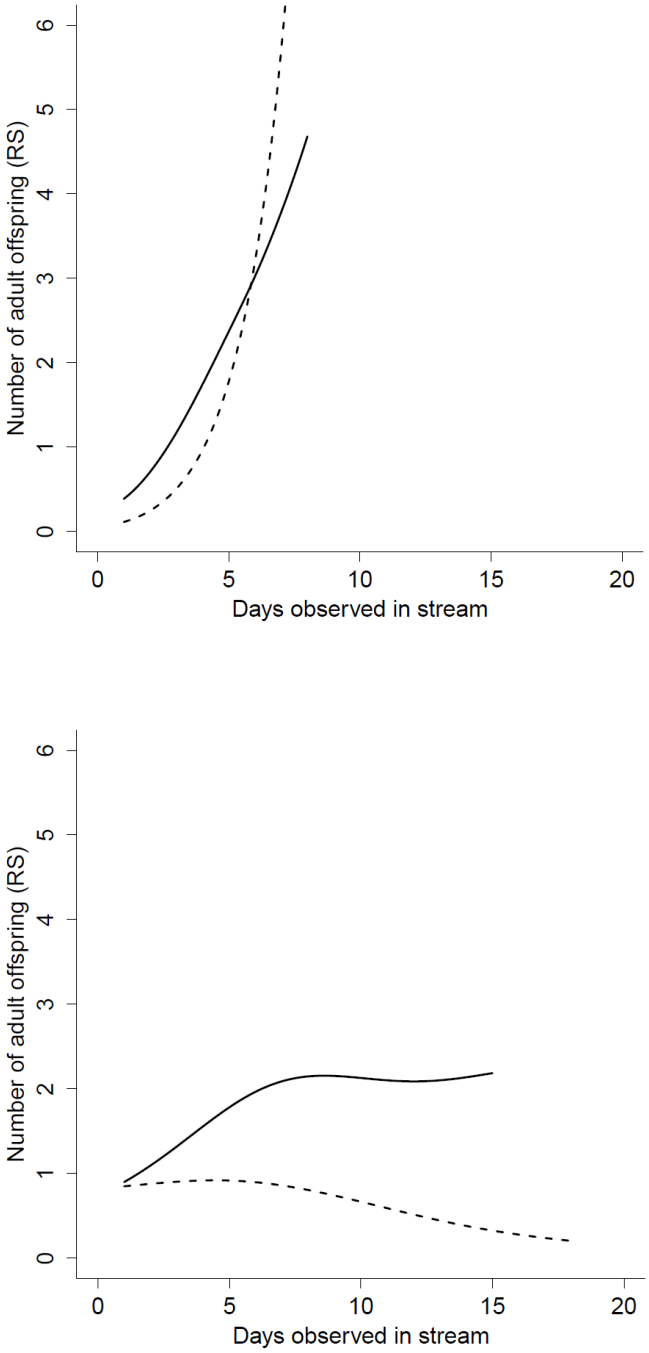


Figure 3.14. Cubic splines describing the relationship between number of days observed in the stream and reproductive success, for female (solid line) and male (dashed line) candidate parents sampled in 2004. The A Creek splines are on top, and C Creek splines are on the bottom.

Table 3.1. Summary of phenotypic traits: body length, body depth, date of first entry into the creek, in-stream lifespan, proportion of days observed in the spawning stream (PropDO), and total number of days observed in the spawning stream (DaysObs). Data in trait columns are means with standard deviation in parentheses. RS is an abbreviation for individual reproductive success (number of adult offspring produced per spawner), and *I* is the opportunity for selection (see text for definition).

Creek	Sex	Year	N	Age 3	Age 4	Age 5	Length (mm)	Depth (mm)	Std Depth (mm)	Date (days)	Lifespan (days)	PropDO	DaysObs	RS	*I*
A	F	2004	388	0	80	0	411.7 (19.3)	104.8 (7.3)	113.8 (7.0)	Aug 10 (6.5)	3.2 (2.5)	0.89 (0.20)	2.4 (1.2)	0.40 (1.4)	9.08
		2008	158	0	87	12	411.5 (26.7)	104.5 (10.3)	112.5 (12.2)	Aug 14 (4.6)	5.1 (3.7)	0.90 (0.18)	4.1 (2.9)		
A	M	2004	161	0	30	0	411.3 (25.0)	119.0 (11.7)	132.7 (9.0)	Aug 7 (6.1)	3.5 (3.3)	0.88 (0.21)	2.4 (1.3)	0.96 (5.0)	5.42
		2008	86	1	24	4	420.4 (37.3)	127.1 (15.7)	137.4 (9.8)	Aug 12 (4.6)	5.7 (3.5)	0.89 (0.18)	4.9 (3.0)		
C	F	2004	307	0	49	3	414.0 (19.9)	105.9 (8.0)	115.9 (6.9)	Aug 5 (5.3)	9.3 (6.0)	0.77 (0.22)	6.0 (4.0)	0.82 (6.4)	9.50
		2008	319	1	223	9	412.0 (21.9)	105.3 (9.4)	115.4 (9.8)	Aug 11 (4.7)	11.2 (6.4)	0.84 (0.17)	9.0 (5.3)		
C	M	2004	156	0	19	1	419.5 (26.4)	124.1 (12.9)	136.5 (9.7)	Aug 2 (4.7)	8.6 (5.8)	0.80 (0.22)	5.8 (3.6)	1.69 (21.8)	7.64
		2008	172	0	96	12	422.7 (29.0)	132.6 (16.5)	143.7 (10.5)	Aug 8 (3.9)	11.2 (5.2)	0.85 (0.16)	9.3 (4.4)		

Table 3.2. Linear correlations between traits, based on data from 2004 A Creek fish. Asterisks indicate significance at α=0.05, and with no corrections for multiple tests applied.

Creek	Sex	Variable 1	Variable 2	Coeff.	r^2	*F*	*P*
A	f	Length	Depth	1.31	0.24	110.09	< 0.001*
		Length	Std depth	-0.39	0.02	6.96	0.009*
		First day	Length	-0.79	0.07	28.32	< 0.001*
		First day	Depth	-0.16	0.02	6.98	0.009*
		First day	Std depth	0.01	0.00	0.05	0.832
		Lifespan	Length	0.00	0.00	0.35	0.552
		Lifespan	Depth	0.00	0.00	0.02	0.875
		Lifespan	Std depth	-0.01	0.00	0.23	0.635
		Lifespan	FirstDay	-0.01	0.00	0.18	0.676
		DaysObs	Length	0.00	0.00	0.03	0.871
		DaysObs	Depth	0.01	0.00	0.84	0.361
		DaysObs	Std depth	0.00	0.00	0.01	0.906
		DaysObs	FirstDay	0.00	0.00	0.12	0.724
		Lifespan	DaysObs	0.34	0.57	514.21	< 0.001*
		DaysObs	PropDO	-2.07	0.12	55.11	< 0.001*
		Lifespan	PropDO	-10.10	0.60	233.67	< 0.001*
A	m	Length	Depth	1.47	0.47	127.21	< 0.001*
		Length	Std depth	-0.19	0.00	0.67	0.42
		First day	Length	-0.87	0.05	7.40	0.007*
		First day	Depth	-0.23	0.01	2.12	0.148
		First day	Std depth	0.19	0.02	2.19	0.142
		Lifespan	Length	-0.01	0.01	1.77	0.185
		Lifespan	Depth	-0.03	0.01	1.55	0.216
		Lifespan	Std depth	-0.02	0.00	0.51	0.476
		Lifespan	FirstDay	-0.04	0.01	0.94	0.333
		DaysObs	Length	-0.01	0.01	2.08	0.151
		DaysObs	Depth	-0.02	0.03	3.77	0.054*
		DaysObs	Std depth	-0.02	0.01	1.92	0.168
		DaysObs	FirstDay	0.01	0.00	0.46	0.500
		Lifespan	DaysObs	0.28	0.48	152.27	< 0.001*
		DaysObs	PropDO	-2.48	0.16	30.56	< 0.001*
		Lifespan	PropDO	-12.68	0.66	318.20	< 0.001*

Table 3.3. Linear correlations between traits, based on data from 2004 C Creek fish. Asterisks indicate significance at α=0.05, and with no corrections for multiple tests applied.

Creek	Sex	Variable 1	Variable 2	Coeff.	r^2	*F*	*P*
C	f	Length	Depth	1.54	0.38	184.72	< 0.001*
		Length	Std depth	-0.25	0.01	2.25	0.013
		First day	Length	-0.94	0.06	19.81	< 0.001*
		First day	Depth	-0.14	0.01	2.74	0.099
		First day	Std depth	0.11	0.01	1.84	0.176
		Lifespan	Length	0.01	0.00	0.20	0.652
		Lifespan	Depth	-0.02	0.00	0.15	0.701
		Lifespan	Std depth	-0.05	0.00	0.96	0.327
		Lifespan	FirstDay	-0.43	0.14	52.15	< 0.001*
		DaysObs	Length	0.01	0.00	0.48	0.491
		DaysObs	Depth	-0.03	0.00	0.98	0.324
		DaysObs	Std depth	-0.06	0.01	3.56	0.060
		DaysObs	FirstDay	-0.26	0.12	42.57	< 0.001*
		Lifespan	DaysObs	0.52	0.61	478.40	< 0.001*
		DaysObs	PropDO	-0.02	0.00	0.00	0.983
		Lifespan	PropDO	-13.62	0.26	106.94	< 0.001*
C	m	Length	Depth	1.46	0.51	144.68	< 0.001*
		Length	Std depth	-0.41	0.02	3.20	0.076
		First day	Length	-0.97	0.03	4.52	0.035*
		First day	Depth	-0.72	0.07	11.00	0.001*
		First day	Std depth	-0.19	0.01	0.81	0.369
		Lifespan	Length	0.01	0.00	0.36	0.551
		Lifespan	Depth	-0.02	0.00	0.20	0.656
		Lifespan	Std depth	-0.09	0.03	4.07	0.046
		Lifespan	FirstDay	-0.09	0.00	0.76	0.384
		DaysObs	Length	0.00	0.00	0.02	0.896
		DaysObs	Depth	-0.01	0.00	0.17	0.681
		DaysObs	Std depth	-0.03	0.01	1.21	0.274
		DaysObs	FirstDay	0.02	0.00	0.15	0.700
		Lifespan	DaysObs	0.48	0.60	233.67	< 0.001*
		DaysObs	PropDO	-2.33	0.02	3.21	0.075
		Lifespan	PropDO	-17.23	0.42	113.09	0.005*

Table 3.4. Mean phenotypic trait values for bear-killed (bk) versus senescent (sen) individuals in each stream for 2004, with *N* denoting sample size. The compared traits are, body length (Length), body depth (Abs=absolute and Std=standardized), in-stream lifespan (Lifespan), number of days observed in the stream (DaysObs), proportion of daily surveys in which an individual was observed during its in-stream lifespan (PropDO), the day of first stream entry (FirstDay), and the number of adult offspring produced (AdultOff).

Stream	Sex	Death	*N*	Length	Abs depth	Std depth	Lifespan	DaysObs	PropDO	FirstDay	AdultOff
A	f	bk	324	412.4	105.0	113.8	3.2	2.4	0.89	Aug 11	0.4
A	f	sen	4	407.5	103.0	112.9	6.3	3.8	0.83	Aug 12	0.8
A	m	bk	128	412.8	119.2	131.9	3.3	2.4	0.88	Aug 9	0.8
A	m	sen	2	345.5	109.5	148.8	5.5	3.0	0.62	Aug 16	0.5
C	f	bk	156	417.1	106.8	116.1	8.5	5.4	0.76	Aug 6	0.8
C	f	sen	63	414.2	105.7	115.6	12.7	8.5	0.73	Aug 5	0.9
C	m	bk	78	420.6	124.8	136.6	6.5	4.7	0.84	Aug 1	2.1
C	m	sen	22	411.0	121.1	136.4	13.3	9.0	0.75	Aug 2	1.0

Table 3.5. Assignment success for A and C creek offspring-parent relationships, with numbers of offspring falling into a particular assignment category.

	A Creek	C Creek
Both parents assigned	146	262
Only mother assigned	18	75
Only father assigned	6	22
No parents assigned	74	60

Table 3.6. Non-standardized selection differentials for each sex within each stream, calculated as the trait mean of selected adults (that produced at least one returning adult offspring) minus the trait mean of all adults.

Creek	Sex	Length (mm)	Abs depth (mm)	Std depth (mm)	Date (days)	Lifespan (days)	Days observed (days)
A	F	-2.15	-0.33	0.00	1.75	1.33	0.87
A	M	-6.73	-0.49	1.53	3.38	0.95	0.53
C	F	-1.12	-0.27	0.16	2.13	0.90	-0.60
C	M	-0.26	-1.08	-1.46	1.57	2.01	1.42

Table 3.7. Standardized selection differentials for each sex within each stream, calculated as the trait mean of selected adults (that produced at least one returning adult offspring) minus the trait mean of all adults, divided by the standard deviation of the trait for all adults.

Creek	Sex	Length (mm)	Abs depth (mm)	Std depth (mm)	Date (days)	Lifespan (days)	Days observed (days)
A	F	-0.11	-0.04	0.00	0.26	0.52	0.11
A	M	-0.28	-0.08	0.17	0.58	0.27	0.28
C	F	-0.03	-0.03	0.02	0.39	0.17	-0.03
C	M	-0.04	-0.14	-0.15	0.54	0.31	0.04

Table 3.8. AIC values for different regression models using trait set 1 (absolute body depth, day of first stream entry, and reproductive lifespan). "Reproductive lifespan" refers to the measure of reproductive lifespan used in the model. For the regression, OLS = ordinary least squares, and ZINB = zero-inflated negative binomial. The AIC values are for the linear and quadratic models, and an NA value indicates that the regression model did not converge.

Stream	Sex	Reproductive lifespan	Regression	Linear AIC	Quad. AIC
A	F	In-stream lifespan	OLS	1774.4	640.3
A	F	Days observed	OLS	1766.6	640.9
A	F	In-stream lifespan	ZINB	510.9	349
A	F	Days observed	ZINB	497.6	350.2
A	M	In-stream lifespan	OLS	634.6	640.3
A	M	Days observed	OLS	631.8	640.9
A	M	In-stream lifespan	ZINB	345.6	349
A	M	Days observed	ZINB	349.2	350.2
C	F	In-stream lifespan	OLS	1504.8	690.3
C	F	Days observed	OLS	1509.2	688.5
C	F	In-stream lifespan	ZINB	515.1	371.7
C	F	Days observed	ZINB	521.9	350.3
C	M	In-stream lifespan	OLS	683.8	690.3
C	M	Days observed	OLS	685.3	688.5
C	M	In-stream lifespan	ZINB	363.9	371.7
C	M	Days observed	ZINB	NA	350.3

Table 3.9. AIC values for different regression models using trait set 2 (body length, standardized body depth, day of first stream entry, and reproductive lifespan). "Reproductive lifespan" refers to the measure of reproductive lifespan used in the model. For the regression, OLS = ordinary least squares, and ZINB = zero-inflated negative binomial. The AIC values are for the linear and quadratic models, and an NA value indicates that the regression model did not converge.

Stream	Sex	Reproductive lifespan	Regression	Linear AIC	Quad. AIC
A	F	In-stream lifespan	OLS	1776.4	643.5
A	F	Days observed	OLS	1768.5	643.2
A	F	In-stream lifespan	ZINB	513.6	355.4
A	F	Days observed	ZINB	500.2	349.0
A	M	In-stream lifespan	OLS	632.8	643.5
A	M	Days observed	OLS	629.9	643.2
A	M	In-stream lifespan	ZINB	347.5	355.4
A	M	Days observed	ZINB	347.8	349.0
C	F	In-stream lifespan	OLS	1501.8	696.7
C	F	Days observed	OLS	1506.4	692.9
C	F	In-stream lifespan	ZINB	517.7	381.1
C	F	Days observed	ZINB	515.8	349.0
C	M	In-stream lifespan	OLS	684.5	696.7
C	M	Days observed	OLS	685.6	692.9
C	M	In-stream lifespan	ZINB	NA	381.1
C	M	Days observed	ZINB	366.1	NA

Table 3.10. Directional selection gradients for the second set of traits (body length, standardized body depth, date of first entry into the stream, reproductive lifespan) with days observed as the measure of reproductive lifespan. β is the selection coefficient, SE is the standard error, *t* is the t-statistic, and *P* is the p-value. An "OLS" subscript denotes estimates from ordinary least-squares regression, and a "ZI" subscript denotes estimates from a zero-inflated Poisson regression analysis. NAs indicate that a regression could not be fit, due to lack of model convergence. Asterisks denote significant gradients ($P < 0.05$).

A Creek

Sex	Trait	β_{OLS}	SE_{OLS}	t_{OLS}	P_{OLS}	β_{ZI}	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Body length	-0.11	0.17	-0.62	0.53	-0.37	0.22	-1.65	0.10
	Std. body depth	-0.08	0.17	-0.47	0.64	-0.07	0.20	-0.36	0.72
	Entry date	0.32	0.17	1.87	0.06	-0.12	0.21	-0.56	0.58
	Days observed	-0.11	0.17	-0.62	0.53	-0.27	0.21	-1.31	0.19
Males	Body length	-0.11	0.20	-0.55	0.59	0.22	0.20	1.07	0.28
	Std. body depth	0.08	0.20	0.42	0.68	-0.27	0.20	-1.39	0.17
	Entry date	0.75	0.19	3.89	0.00*	0.61	0.21	2.84	0.00*
	Days observed	0.47	0.20	2.32	0.02*	0.30	0.22	1.40	0.16

C Creek

Sex	Trait	β_{OLS}	SE_{OLS}	t_{OLS}	P_{OLS}	β_{ZI}	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Body length	0.10	0.19	0.53	0.60	-0.16	0.30	-0.53	0.60
	Std. body depth	-0.09	0.19	-0.48	0.63	-0.15	0.24	-0.63	0.53
	Entry date	0.34	0.21	1.66	0.10	0.07	0.32	0.23	0.82
	Days observed	-0.05	0.20	-0.27	0.79	0.07	0.35	0.19	0.85
Males	Body length	0.16	0.24	0.67	0.50	0.28	0.32	0.87	0.39
	Std. body depth	-0.27	0.24	-1.10	0.27	-0.13	0.31	-0.43	0.67
	Entry date	0.55	0.24	2.27	0.02*	-0.11	0.36	-0.29	0.77
	Days observed	0.01	0.26	0.05	0.96	-0.28	0.37	-0.75	0.45

Table 3.11. Nonlinear selection gradients for the second set of traits (body length, standardized body depth, date of first entry into the stream, reproductive lifespan) with days observed as the measure of reproductive lifespan. Coeff indicates the selection coefficient, γ is the quadratic selection gradient, SE is the standard error, *t* is the t-statistic, and *P* is the p-value. An "OLS" subscript denotes estimates from ordinary least-squares regression, and a "ZI" subscript denotes estimates from a zero-inflated negative binomial regression analysis. Asterisks denote significant gradients ($P < 0.05$).

A Creek

Sex	Trait	$Coeff_{OLS}$	γ_{OLS}	SE_{OLS}	t_{OLS}	P_{OLS}	$Coeff_{ZI}$	γ_{ZI}	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Body length^2	-0.21	-0.42	0.12	-1.76	0.08	-0.63	-1.26	0.16	-3.95	0.00*
	Std body depth^2	-0.04	-0.08	0.10	-0.43	0.66	-0.13	-0.26	0.13	-0.99	0.32
	Entry date^2	-0.58	-1.16	0.19	-3.02	0.00*	-0.52	-1.04	0.20	-2.57	0.01*
	Days observed^2	-0.17	-0.34	0.10	-1.67	0.10	0.49	0.98	0.18	2.69	0.01*
	Length x std depth	-0.23	NA	0.14	-1.64	0.10	-0.52	NA	0.21	-2.53	0.01*
	Length x date	-0.30	NA	0.19	-1.58	0.12	-0.41	NA	0.23	-1.78	0.08
	Length x days	-0.09	NA	0.21	-0.45	0.66	-0.18	NA	0.19	-0.93	0.36
	Std depth x date	-0.24	NA	0.19	-1.31	0.19	-0.08	NA	0.19	-0.43	0.67
	Std depth x days	0.06	NA	0.20	0.33	0.74	-0.02	NA	0.19	-0.09	0.93
	Date x days	-0.02	NA	0.19	-0.13	0.90	-0.10	NA	0.28	-0.37	0.71
Males	Body length^2	-0.17	-0.34	0.11	-1.61	0.11	-0.31	-0.62	0.13	-2.33	0.02*
	Std body depth^2	0.01	0.02	0.15	0.08	0.94	0.14	0.28	0.15	0.91	0.36
	Entry date^2	0.01	0.02	0.20	0.03	0.98	-0.21	-0.42	0.15	-1.35	0.18
	Days observed^2	-0.12	-0.24	0.15	-0.81	0.42	0.11	0.22	0.15	0.75	0.45
	Length x std depth	0.00	NA	0.23	0.02	0.98	-0.14	NA	0.18	-0.78	0.44
	Length x date	-0.17	NA	0.21	-0.82	0.42	0.14	NA	0.20	0.71	0.48
	Length x days	-0.05	NA	0.29	-0.18	0.86	0.63	NA	0.25	2.54	0.01*
	Std depth x date	0.14	NA	0.23	0.61	0.54	0.25	NA	0.22	1.16	0.25
	Std depth x days	0.02	NA	0.22	0.07	0.94	0.57	NA	0.22	2.65	0.01*
	Date x days	0.19	NA	0.24	0.77	0.44	-0.01	NA	0.27	-0.03	0.98

Table 3.11, continued.

C Creek

Sex	Trait	$Coeff_{OLS}$	γ_{OLS}	SE_{OLS}	t_{OLS}	P_{OLS}	$Coeff_{ZI}$	γ_{ZI}	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Body length^2	-0.17	-0.34	0.12	-1.35	0.18	-0.83	-1.66	0.24	-3.49	0.00*
	Std body depth^2	0.01	0.02	0.13	0.08	0.94	-0.57	-1.14	0.22	-2.63	0.01*
	Entry date^2	-0.20	-0.40	0.17	-1.17	0.24	-1.93	-3.86	0.42	-4.54	0.00*
	Days observed^2	-0.31	-0.62	0.19	-1.63	0.11	-0.51	-1.02	0.36	-1.42	0.16
	Length x std depth	-0.02	NA	0.17	-0.10	0.92	-1.31	NA	0.38	-3.44	0.00*
	Length x date	-0.23	NA	0.25	-0.93	0.36	-0.74	NA	0.39	-1.90	0.06
	Length x days	0.05	NA	0.25	0.19	0.85	-0.93	NA	0.59	-1.59	0.11
	Std depth x date	-0.02	NA	0.22	-0.11	0.91	-0.40	NA	0.36	-1.14	0.25
	Std depth x days	0.07	NA	0.23	0.31	0.75	-0.48	NA	0.52	-0.92	0.36
	Date x days	-0.41	NA	0.30	-1.38	0.17	-1.78	NA	0.48	-3.69	0.00*
Males	Body length^2	-0.17	-0.34	0.19	-0.88	0.38	NA	NA	NA	NA	NA
	Std body depth^2	-0.11	-0.22	0.16	-0.69	0.49	NA	NA	NA	NA	NA
	Entry date^2	-0.37	-0.74	0.18	-2.08	0.04*	NA	NA	NA	NA	NA
	Days observed^2	0.17	-0.34	0.24	0.71	0.48	NA	NA	NA	NA	NA
	Length x std depth	-0.11	NA	0.26	-0.45	0.66	NA	NA	NA	NA	NA
	Length x date	0.12	NA	0.28	0.42	0.68	NA	NA	NA	NA	NA
	Length x days	0.21	NA	0.31	0.68	0.50	NA	NA	NA	NA	NA
	Std depth x date	-0.63	NA	0.34	-1.85	0.07	NA	NA	NA	NA	NA
	Std depth x days	0.46	NA	0.29	1.60	0.11	NA	NA	NA	NA	NA
	Date x days	-0.42	NA	0.36	-1.15	0.25	NA	NA	NA	NA	NA

Table 3.12. Heritabilities (h^2) estimated using parent-offspring regression, and the standard error (SE) for the estimate.

Trait	Creek	Sex	h^2	SE
Body length	A	f	0.23	0.26
Body depth (abs)	A	f	-0.15	0.28
Body depth (std)	A	f	0.37	0.30
Entry date	A	f	0.78	0.12
In-stream lifespan	A	f	-0.05	0.27
Days observed	A	f	-0.22	0.53
Body length	A	m	0.26	0.36
Body depth (abs)	A	m	0.58	0.91
Body depth (std)	A	m	0.37	0.30
Entry date	A	m	0.70	0.21
In-stream lifespan	A	m	0.01	0.31
Days observed	A	m	-0.07	0.61
Body length	C	f	0.00	0.12
Body depth (abs)	C	f	0.44	0.13
Body depth (std)	C	f	0.35	0.12
Entry date	C	f	0.55	0.11
In-stream lifespan	C	f	0.28	0.14
Days observed	C	f	0.39	0.17
Body length	C	m	0.42	0.18
Body depth (abs)	C	m	0.29	0.20
Body depth (std)	C	m	0.11	0.22
Entry date	C	m	0.55	0.11
In-stream lifespan	C	m	0.03	0.16
Days observed	C	m	0.17	0.19

Table 3.13. Heritabilities (h^2) estimated using MCMCglmm, with "mother" modeled as a random effect and "sex" modeled as a fixed effect. Lower CI is the lower bound and Upper CI is the upper bound of the 95% confidence interval.

Trait	Creek	h^2	Lower CI	Upper CI
Body length	A	0.16	0.08	0.76
Body depth (abs)	A	0.19	0.08	0.58
Body depth (std)	A	0.25	0.08	0.57
Entry date	A	0.61	0.26	0.92
Lifespan	A	0.15	0.05	0.46
Days observed	A	0.20	0.04	0.60
Body length	C	0.11	0.06	0.44
Body depth (abs)	C	0.22	0.08	0.40
Body depth (std)	C	0.17	0.09	0.40
Entry date	C	0.28	0.14	0.64
Lifespan	C	0.15	0.06	0.39
Days observed	C	0.17	0.06	0.43

Table 3.14. Responses to selection based on the univariate breeder's equation, calculated using the estimated heritabilities (Table 3.13) and non-standardized selection differentials (Table 3.6).

Creek	Sex	Length (mm)	Absolute depth (mm)	Standardized depth (mm)	Date (days)	Lifespan (days)	Days observed (days)
A	F	-0.34	-0.06	0.00	1.07	0.20	0.17
A	M	-1.08	-0.09	0.38	2.06	0.14	0.11
C	F	-0.12	-0.06	0.03	0.60	0.14	-0.10
C	M	-0.03	-0.24	-0.25	0.44	0.30	0.24

Table 3.S1. Summary of genotype data for A Creek. *N* is the number of samples, *H*o and *H*e are observed and expected heterozygosities, F_{IS} is the inbreeding coefficient (Weir & Cockerham 1984), *HWE* is the probability of being out of Hardy-Weinberg equilibrium due to heterozygote deficiency, and *AR* is allelic richness.

Sample	Locus	*N*	*H*o	*H*e	F_{IS}	*HWE*	*AR*
A Creek 2004	One100	493	0.70	0.81	0.14	0.00	12.42
	One102	520	0.83	0.84	0.01	0.00	12.73
	One103	513	0.88	0.91	0.04	0.10	23.55
	One106	458	0.78	0.88	0.11	0.00	21.23
	One108	512	0.85	0.85	0.00	0.28	12.58
	One109	517	0.77	0.76	-0.01	0.47	9.37
	One110c	511	0.83	0.80	-0.05	0.18	10.93
	One111	469	0.74	0.79	0.07	0.00	11.65
	Ots103	518	0.85	0.85	0.00	0.67	12.96
	One114	520	0.90	0.88	-0.02	0.89	14.91
	One115	453	0.69	0.89	0.23	0.00	13.66
A Creek 2008	One100	205	0.68	0.83	0.18	0.00	12.86
	One102	211	0.83	0.86	0.03	0.00	12.00
	One103	219	0.86	0.91	0.05	0.00	30.10
	One106	191	0.84	0.89	0.06	0.03	25.00
	One108	217	0.87	0.86	0.00	0.18	15.63
	One109	216	0.77	0.78	0.01	0.06	12.86
	One110c	215	0.83	0.84	0.01	0.46	11.89
	One111	194	0.86	0.80	-0.08	0.80	17.89
	Ots103	219	0.87	0.87	0.01	0.13	13.00
	One114	218	0.85	0.89	0.04	0.18	16.84
	One115	194	0.77	0.89	0.13	0.00	15.97

Table 3.S2. Summary of genotype data for C Creek. *N* is the number of samples, *H*o and *H*e are observed and expected heterozygosities, F_{IS} is the inbreeding coefficient (Weir & Cockerham 1984), *HWE* is the probability of being out of Hardy-Weinberg equilibrium due to heterozygote deficiency, and *AR* is allelic richness.

Sample	Locus	*N*	*H*o	*H*e	F_{IS}	*HWE*	*AR*
C Creek 2004	One100	357	0.74	0.85	0.13	0.00	15.12
	One102	338	0.86	0.84	-0.02	0.00	12.75
	One103	364	0.95	0.93	-0.02	0.00	27.86
	One106	363	0.72	0.86	0.16	0.00	19.54
	One108	351	0.86	0.87	0.02	0.00	17.22
	One109	364	0.81	0.81	0.00	0.00	10.67
	One110c	359	0.84	0.83	-0.02	0.07	12.59
	One111	364	0.66	0.68	0.02	0.03	19.85
	Ots103	339	0.83	0.85	0.03	0.00	14.80
	One114	364	0.85	0.87	0.02	0.03	16.03
	One115	351	0.81	0.89	0.09	0.00	16.49
C Creek 2008	One100	464	0.72	0.88	0.18	0.00	15.74
	One102	455	0.86	0.84	-0.03	0.04	14.37
	One103	465	0.88	0.93	0.05	0.00	29.99
	One106	464	0.59	0.87	0.32	0.00	23.87
	One108	456	0.89	0.87	-0.02	0.00	16.51
	One109	465	0.77	0.82	0.06	0.00	11.88
	One110c	463	0.84	0.85	0.01	0.03	14.46
	One111	469	0.77	0.74	-0.04	0.06	21.10
	Ots103	447	0.86	0.86	0.01	0.00	16.22
	One114	468	0.84	0.87	0.03	0.00	17.24
	One115	455	0.80	0.90	0.11	0.00	16.07

Table 3.S3. Means and standard deviations of predation indices for spatial and temporal divisions within each stream (Fig. 2.2 shows the divisions).

Spatial division	Mean	StdDev
A1	0.43	0.39
A2	0.43	0.43
A3	0.37	0.42
A4	0.37	0.42
C1	0.21	0.36
C2	0.18	0.30
C3	0.32	0.42

Temporal division	Mean	StdDev
A1	0.37	0.22
A2	0.50	0.30
A3	0.42	0.31
A4	0.14	0.16
C1	0.35	0.38
C2	0.08	0.19
C3	0.25	0.29

Table 3.S4. Directional selection gradients for first set of traits (absolute body depth, date of first entry into the stream, reproductive lifespan) with in-stream lifespan as the measure of reproductive lifespan. β is the selection coefficient, SE is the standard error, *t* is the t-statistic, and *P* is the p-value. An "OLS" subscript denotes estimates from ordinary least-squares regression, and a "ZI" subscript denotes estimates from a zero-inflated negative binomial regression analysis. Asterisks denote significant gradients ($P < 0.05$).

A Creek

Sex	Trait	β_{OLS}	SE_{OLS}	t_{OLS}	P_{OLS}	β_{ZI}	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Abs. body depth	-0.01	0.03	-0.38	0.71	-0.21	0.21	-1.02	0.31
	Entry date	-0.04	0.03	-1.31	0.19	-0.13	0.24	-0.54	0.59
	Lifespan	-0.08	0.03	-2.55	0.01*	-0.28	0.19	-1.49	0.14
Males	Abs. body depth	-0.04	0.05	-0.87	0.39	-0.15	0.20	-0.76	0.45
	Entry date	-0.13	0.05	-2.61	0.01*	0.23	0.20	1.10	0.27
	Lifespan	-0.09	0.05	-1.90	0.06	-0.13	0.21	-0.63	0.53

C Creek

Sex	Trait	β_{OLS}	SE_{OLS}	t_{OLS}	P_{OLS}	B_{ZI}	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Abs. body depth	0.04	0.18	0.20	0.84	-0.01	0.22	-0.05	0.96
	Entry date	0.50	0.20	2.52	0.01*	-0.02	0.27	-0.09	0.93
	Lifespan	0.42	0.20	2.10	0.04*	0.11	0.27	0.41	0.68
Males	Abs. body depth	-0.04	0.25	-0.16	0.88	-0.07	0.33	-0.20	0.84
	Entry date	0.58	0.24	2.40	0.02*	0.13	0.35	0.37	0.71
	Lifespan	0.32	0.26	1.21	0.23	0.31	0.37	0.86	0.39

Table 3.S5. Directional selection gradients for the second set of traits (body length, standardized body depth, date of first entry into the stream, reproductive lifespan) with in-stream lifespan as the measure of reproductive lifespan. β is the selection coefficient, SE is the standard error, *t* is the t-statistic, and *P* is the p-value. An "OLS" subscript denotes estimates from ordinary least-squares regression, and a "ZI" subscript denotes estimates from a zero-inflated Poisson regression analysis. NAs indicate that a regression could not be fit, due to lack of model convergence. Asterisks denote significant gradients ($P < 0.05$).

A Creek

Sex	Trait	β_{OLS}	SE_{OLS}	t_{OLS}	P_{OLS}	β_{ZI}	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Body length	0.01	0.03	0.32	0.75	-0.32	0.21	-1.52	0.13
	Std. body depth	-0.02	0.03	-0.67	0.51	-0.12	0.19	-0.67	0.50
	Entry date	-0.04	0.03	-1.15	0.25	-0.16	0.24	-0.69	0.49
	Lifespan	-0.08	0.03	-2.55	0.01*	-0.26	0.17	-1.46	0.14
Males	Body length	0.00	0.05	0.07	0.95	0.14	0.22	0.66	0.51
	Std. body depth	-0.06	0.05	-1.30	0.20	-0.25	0.20	-1.25	0.21
	Entry date	-0.12	0.05	-2.32	0.02*	0.50	0.25	1.99	0.05*
	Lifespan	-0.09	0.05	-1.86	0.07	0.04	0.23	0.17	0.86

C Creek

Sex	Trait	β_{OLS}	SE_{OLS}	t_{OLS}	P_{OLS}	β_{ZI}	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Body length	0.15	0.19	0.76	0.45	0.19	0.26	0.74	0.46
	Std. body depth	-0.07	0.19	-0.39	0.69	-0.07	0.18	-0.36	0.72
	Entry date	0.55	0.21	2.66	0.01*	0.09	0.28	0.31	0.76
	Lifespan	0.44	0.20	2.14	0.03*	0.12	0.26	0.45	0.65
Males	Body length	0.17	0.24	0.68	0.50	NA	NA	NA	NA
	Std. body depth	-0.22	0.25	-0.91	0.37	NA	NA	NA	NA
	Entry date	0.58	0.24	2.40	0.02*	NA	NA	NA	NA
	Lifespan	0.28	0.27	1.06	0.29	NA	NA	NA	NA

Table 3.S6. Directional selection gradients for the first set of traits (absolute body depth, date of first entry into the stream, reproductive lifespan) with days observed as the measure of reproductive lifespan. β is the selection coefficient, SE is the standard error, *t* is the t-statistic, and *P* is the p-value. An "OLS" subscript denotes estimates from ordinary least-squares regression, and a "ZI" subscript denotes estimates from a zero-inflated negative binomial regression analysis. NAs indicate that a regression could not be fit, due to lack of model convergence. Asterisks denote significant gradients ($P < 0.05$).

A Creek

Sex	Trait	β_{OLS}	SE_{OLS}	t_{OLS}	P_{OLS}	β_{ZI}	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Abs. body depth	-0.12	0.17	-0.68	0.50	-0.12	0.20	-0.63	0.53
	Entry date	0.33	0.17	1.96	0.05*	0.06	0.20	0.31	0.76
	Days observed	0.62	0.18	3.50	0.00*	-0.33	0.14	-2.40	0.02*
Males	Abs. body depth	-0.02	0.19	-0.10	0.92	-0.10	0.21	-0.46	0.64
	Entry date	0.78	0.19	4.18	0.00*	0.29	0.21	1.39	0.16
	Days observed	0.47	0.20	2.35	0.02*	0.17	0.24	0.70	0.49

C Creek

Sex	Trait	β_{OLS}	SE_{OLS}	t_{OLS}	P_{OLS}	β_{ZI}	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Abs. body depth	0.00	0.18	0.01	0.99	-0.07	0.27	-0.24	0.81
	Entry date	0.31	0.20	1.55	0.12	0.12	0.31	0.39	0.70
	Days observed	-0.05	0.20	-0.25	0.80	-0.03	0.35	-0.10	0.92
Males	Abs. body depth	-0.08	0.25	-0.31	0.76	NA	NA	NA	NA
	Entry date	0.54	0.24	2.25	0.03*	NA	NA	NA	NA
	Days observed	0.02	0.26	0.09	0.93	NA	NA	NA	NA

Table 3.S7. Nonlinear selection gradients for the first set of traits (absolute body depth, date of first entry into the stream, reproductive lifespan) with in-stream lifespan as the measure of reproductive lifespan. β is the selection coefficient, SE is the standard error, *t* is the t-statistic, and *P* is the p-value. An "OLS" subscript denotes estimates from ordinary least-squares regression, and a "ZI" subscript denotes estimates from a zero-inflated negative binomial regression analysis. NAs indicate that a regression could not be fit, due to lack of model convergence. Asterisks denote significant gradients ($P < 0.05$).

A Creek

Sex	Trait	$Coeff_{OLS}$	SE_{OLS}	t_{OLS}	P_{OLS}	$Coeff_{ZI}$	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Body depth^2	0.02	0.02	0.89	0.38	-0.32	0.17	-1.92	0.05
	Entry date^2	0.05	0.03	1.61	0.11	-0.28	0.21	-1.33	0.18
	Lifespan^2	0.04	0.02	2.09	0.04*	0.33	0.14	2.38	0.02*
	Depth x date	0.05	0.03	1.60	0.11	0.06	0.23	0.24	0.81
	Depth x lifespan	-0.02	0.03	-0.69	0.49	0.15	0.22	0.71	0.48
	Date x lifespan	0.01	0.04	0.19	0.85	0.16	0.26	0.62	0.53
Males	Body depth^2	0.03	0.03	0.95	0.34	-0.25	0.12	-2.00	0.05*
	Entry date^2	0.01	0.05	0.28	0.78	-0.02	0.20	-0.10	0.92
	Lifespan^2	0.07	0.03	2.68	0.01*	-0.35	0.20	-1.77	0.08
	Depth x date	0.01	0.05	0.23	0.82	0.34	0.19	1.84	0.07
	Depth x lifespan	0.10	0.07	1.55	0.12	0.21	0.29	0.72	0.47
	Date x lifespan	0.15	0.07	2.10	0.04*	-0.17	0.30	-0.58	0.56

Table 3.S7, continued.

C Creek

Sex	Trait	$Coeff_{OLS}$	SE_{OLS}	t_{OLS}	P_{OLS}	$Coeff_{ZI}$	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Body depth^2	-0.07	0.09	-0.72	0.48	0.43	0.28	1.52	0.13
	Entry date^2	-0.04	0.15	-0.28	0.78	1.32	0.54	2.44	0.01*
	Lifespan^2	-0.15	0.21	-0.72	0.47	-1.09	0.32	-3.37	0.00*
	Depth x date	-0.10	0.21	-0.48	0.63	-0.68	0.48	-1.43	0.15
	Depth x lifespan	-0.09	0.23	-0.38	0.71	-0.64	0.36	-1.79	0.07
	Date x lifespan	0.04	0.26	0.17	0.87	-0.84	0.43	-1.98	0.05*
Males	Body depth^2	-0.24	0.21	-1.15	0.25	-0.07	0.18	-0.36	0.72
	Entry date^2	-0.11	0.18	-0.59	0.56	-1.42	0.51	-2.76	0.01*
	Lifespan^2	0.02	0.30	0.05	0.96	0.42	0.42	1.01	0.31
	Depth x date	-0.24	0.29	-0.81	0.42	-0.40	0.68	-0.58	0.56
	Depth x lifespan	0.09	0.27	0.34	0.74	0.00	0.36	0.00	1.00
	Date x lifespan	0.41	0.34	1.20	0.23	-0.28	0.96	-0.29	0.77

Table 3.S8. Nonlinear selection gradients for the second set of traits (body length, standardized body depth, date of first entry into the stream, reproductive lifespan) with in-stream lifespan as the measure of reproductive lifespan. β is the selection coefficient, SE is the standard error, *t* is the t-statistic, and *P* is the p-value. An "OLS" subscript denotes estimates from ordinary least-squares regression, and a "ZI" subscript denotes estimates from a zero-inflated negative binomial regression analysis. NAs indicate that a regression could not be fit, due to lack of model convergence. Asterisks denote significant gradients ($P < 0.05$).

A Creek

Sex	Trait	$Coeff_{OLS}$	SE_{OLS}	t_{OLS}	P_{OLS}	$Coeff_{ZI}$	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Body length^2	0.04	0.02	1.82	0.07	-0.50	0.18	-2.81	0.01
	Std body depth^2	0.00	0.02	-0.19	0.85	-0.14	0.18	-0.79	0.43
	Entry date^2	0.04	0.03	1.15	0.25	-0.44	0.27	-1.65	0.10
	Lifespan^2	0.04	0.02	2.11	0.04*	0.30	0.14	2.17	0.03*
	Length x std depth	0.05	0.03	1.77	0.08	-0.39	0.21	-1.82	0.07
	Length x date	0.01	0.04	0.31	0.76	-0.18	0.27	-0.67	0.50
	Length x lifespan	0.02	0.03	0.46	0.65	-0.07	0.23	-0.31	0.75
	Std depth x date	0.08	0.03	2.34	0.02*	0.03	0.20	0.17	0.86
	Std depth x lifespan	-0.03	0.03	-0.94	0.35	-0.04	0.25	-0.17	0.86
	Date x lifespan	0.02	0.04	0.42	0.68	0.04	0.33	0.12	0.90
Males	Body length^2	0.02	0.03	0.61	0.54	-0.30	0.15	-2.07	0.04*
	Std body depth^2	0.04	0.04	1.12	0.26	0.05	0.16	0.35	0.73
	Entry date^2	0.00	0.05	0.05	0.96	-0.14	0.17	-0.80	0.42
	Lifespan^2	0.07	0.03	2.46	0.02*	-0.20	0.22	-0.92	0.36
	Length x std depth	-0.02	0.05	-0.29	0.77	-0.08	0.19	-0.42	0.68
	Length x date	0.04	0.05	0.81	0.42	0.01	0.23	0.05	0.96
	Length x lifespan	0.08	0.08	1.03	0.31	0.12	0.36	0.34	0.74
	Std depth x date	-0.08	0.06	-1.48	0.14	0.27	0.24	1.14	0.26
	Std depth x lifespan	0.04	0.07	0.52	0.61	0.34	0.22	1.50	0.13
	Date x lifespan	0.15	0.08	1.96	0.05*	-0.14	0.30	-0.46	0.65

Table S3.8, continued.

C Creek

Sex	Trait	$Coeff_{OLS}$	SE_{OLS}	t_{OLS}	P_{OLS}	$Coeff_{ZI}$	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Body length^2	-0.13	0.12	-1.06	0.29	-0.49	0.39	-1.24	0.21
	Std body depth^2	-0.01	0.13	-0.11	0.91	0.30	0.19	1.56	0.12
	Entry date^2	-0.04	0.17	-0.24	0.81	0.10	0.58	0.17	0.87
	Lifespan^2	-0.13	0.21	-0.63	0.53	-0.40	0.42	-0.96	0.34
	Length x std depth	-0.06	0.17	-0.36	0.72	0.02	0.38	0.05	0.96
	Length x date	-0.16	0.25	-0.61	0.54	-1.08	0.49	-2.23	0.03*
	Length x lifespan	0.03	0.24	0.14	0.89	-0.86	0.36	-2.41	0.02*
	Std depth x date	-0.13	0.23	-0.58	0.56	-0.19	0.33	-0.56	0.58
	Std depth x lifespan	-0.19	0.24	-0.78	0.43	0.04	0.38	0.10	0.92
	Date x lifespan	0.06	0.27	0.23	0.82	-0.61	0.33	-1.86	0.06
Males	Body length^2	-0.20	0.20	-0.99	0.32	-0.07	0.13	-0.51	0.61
	Std body depth^2	-0.19	0.17	-1.13	0.26	-0.37	0.20	-1.81	0.07
	Entry date^2	-0.18	0.20	-0.93	0.36	-1.48	0.85	-1.73	0.08
	Lifespan^2	0.10	0.31	0.32	0.75	0.66	0.37	1.76	0.08
	Length x std depth	-0.15	0.26	-0.59	0.56	0.51	0.29	1.75	0.08
	Length x date	0.10	0.28	0.36	0.72	0.13	0.75	0.18	0.86
	Length x lifespan	0.09	0.26	0.35	0.73	0.34	0.29	1.16	0.25
	Std depth x date	-0.51	0.36	-1.41	0.16	0.47	0.94	0.50	0.62
	Std depth x lifespan	-0.05	0.30	-0.16	0.87	-0.01	0.41	-0.02	0.98
	Date x lifespan	0.28	0.36	0.79	0.43	-0.10	1.36	-0.08	0.94

Table 3.S9. Nonlinear selection gradients for the first set of traits (absolute body depth, date of first entry into the stream, reproductive lifespan) with days observed as the measure of reproductive lifespan. β is the selection coefficient, SE is the standard error, *t* is the t-statistic, and *P* is the p-value. An "OLS" subscript denotes estimates from ordinary least-squares regression, and a "ZI" subscript denotes estimates from a zero-inflated negative binomial regression analysis. NAs indicate that a regression could not be fit, due to lack of model convergence. Asterisks denote significant gradients ($P < 0.05$).

A Creek

Sex	Trait	$Coeff_{OLS}$	SE_{OLS}	t_{OLS}	P_{OLS}	$Coeff_{ZI}$	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Body depth^2	-0.16	0.10	-1.49	0.14	-0.36	0.19	-1.91	0.06
	Entry date^2	-0.56	0.18	-3.06	0.00*	-0.36	0.22	-1.65	0.10
	Days observed^2	-0.17	0.10	-1.70	0.09	0.47	0.20	2.40	0.02*
	Depth x date	-0.30	0.18	-1.63	0.10	-0.02	0.24	-0.10	0.92
	Depth x days	0.00	0.20	0.01	0.99	0.17	0.21	0.81	0.42
	Date x days	-0.01	0.18	-0.05	0.96	0.01	0.27	0.03	0.98
Males	Body depth^2	-0.14	0.14	-0.99	0.32	-0.25	0.12	-2.13	0.03*
	Entry date^2	-0.03	0.20	-0.16	0.88	-0.10	0.17	-0.60	0.55
	Days observed^2	-0.13	0.13	-0.98	0.33	-0.19	0.13	-1.43	0.15
	Depth x date	-0.08	0.21	-0.38	0.71	0.35	0.18	1.92	0.06
	Depth x days	-0.09	0.25	-0.35	0.73	0.32	0.25	1.27	0.20
	Date x days	0.11	0.23	0.48	0.63	-0.34	0.25	-1.36	0.18

Table 3.S9, continued.

C Creek

Sex	Trait	$Coeff_{OLS}$	SE_{OLS}	t_{OLS}	P_{OLS}	$Coeff_{ZI}$	SE_{ZI}	t_{ZI}	P_{ZI}
Females	Body depth^2	-0.06	0.09	-0.63	0.53	-1.05	0.23	-4.48	0.00*
	Entry date^2	-0.17	0.15	-1.12	0.26	-2.03	0.44	-4.66	0.00*
	Days observed^2	-0.30	0.19	-1.60	0.11	-0.51	0.32	-1.59	0.11
	Depth x date	-0.09	0.20	-0.44	0.66	-0.75	0.29	-2.62	0.01*
	Depth x days	0.05	0.23	0.21	0.83	-1.11	0.50	-2.21	0.03*
	Date x days	-0.38	0.29	-1.30	0.20	-1.87	0.49	-3.79	0.00*
Males	Body depth^2	-0.16	0.21	-0.78	0.43	-0.40	0.19	-2.08	0.04*
	Entry date^2	-0.34	0.18	-1.93	0.06	-1.72	0.67	-2.56	0.01*
	Days observed^2	0.11	0.23	0.49	0.63	-0.40	0.21	-1.92	0.05*
	Depth x date	-0.34	0.29	-1.17	0.24	1.18	0.63	1.86	0.06
	Depth x days	0.50	0.30	1.66	0.10	1.96	0.53	3.67	0.00*
	Date x days	-0.32	0.36	-0.89	0.38	-4.42	1.62	-2.73	0.01*

Chapter 4: Modeling local adaptation and gene flow in sockeye salmon

Abstract

Microevolutionary processes determine levels of local adaptation within populations and presumably affect population productivity, although evolutionary change has rarely been linked explicitly to population dynamics. Here, we describe a stochastic, individual-based model that simulates evolutionary and demographic effects of gene flow and selection in interconnected sockeye salmon (*Oncorhynchus nerka*) populations. Two populations were simulated, representing beach and stream spawning ecotypes. Individuals undergo a full salmonid life cycle, experiencing sexual selection, size-selective harvest, predation, and natural stabilizing selection based on body length at maturity. Body length, body depth and age at maturity are tracked for each individual, and these three traits evolve 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 affected by the opposing effects of stabilizing and harvest selection; strong stabilizing selection caused the salmon to evolved larger body sizes that made them more likely to be caught by the fishery. The model results suggest that interactions between different selection pressures have substantial evolutionary and demographic consequences, and that the selection pressures affecting wild populations merit further study.

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 divergent selection, opposed by gene flow and temporal variation in selection, confounded by genetic drift, and constrained by genetic variation (Kawecki & Ebert 2004). 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 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 population dynamics is difficult to accomplish empirically (see Coulson *et al.* 2006, Coulson *et al.* 2010, and Pelletier *et al.* 2007 for notable exceptions). A growing body of literature indicates that local adaptation can develop over even 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 datasets without comparable control populations is insufficient, as such data are determined by both genetic and environmental variation, which precludes 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 (e.g. Conover & Munch 2002). Unfortunately, the number of species that can be realistically used for such experiments are limited, and laboratory-induced artifacts may affect results (Harshman & Hoffmann 2000). It is also possible to study wild populations intensively by pedigree analysis, which can provide data on both quantitative genetic parameters (genetic correlations and heritability) and selection gradients (Garant & Kruuk 2005; Pemberton 2008). However, pedigree studies are only feasible for small populations, which 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.

Alternatively, 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 deterministic age- or stage-structured (age-stage-structured) models to simulate consequent effects on population dynamics (Eldridge *et al.* 2010; Law 1991). Integral projection models (IPMs) also predict evolutionary change but are based

on integrals rather than matrices. Thus, IPMs require estimation of fewer parameters (Ellner & Rees 2006) but rely on functions describing the associations between traits and survival, fertility, trait development, and offspring trait values (Coulson *et al.* 2010). Both age-stage-structured models and IPMs are useful for simulating evolutionary and demographic trends over time, but they do not allow for variability among individuals, which can alter evolutionary outcomes (Coulson *et al.* 2004; Wilson 1998). Individual-based models (IBMs) are another type of simulation that is useful for considering variation among individuals due to stochastic events (Grimm 1999), and they can readily incorporate age structure. Although computationally intensive, they provide a very 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).

Combining quantitative genetic and demographic models can provide useful insights into the ecological consequences of potential evolutionary responses in populations. 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 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 simulates a single population of salmon, and population dynamics are affected by survival at different stages that individuals undergo during the Chinook salmon life cycle. Specifically, fish experience 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 are tracked, and empirically-estimated heritabilities for these traits are 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 (Hard *et al.* 2008). Second, we modeled two populations rather than one and allowed for dispersal between the populations to assess the effects of gene flow on local adaptation and population productivity. No previously published IBMs in 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 & Magnuson 1998). Indeed, metapopulation dynamics are thought to affect

salmonid population persistence on both ecological and evolutionary time scales (Schtickzelle & 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 (*O. nerka*) 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). 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 sometimes 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.* 2008a). Thus, interactions between adaptive divergence and gene flow potentially impact evolution and maintenance of these ecotypes.

Our overall aim was to develop and use the 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. The 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. The 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 experiments, we hoped to demonstrate the potential utility of this model in linking evolution and population dynamics.

Materials and methods

Conceptually, the model links evolution and population dynamics as follows. Two sockeye salmon populations linked by gene flow are simulated, one representing the stream ecotype and one representing the beach ecotype. Individuals proceed through a full anadromous salmonid life cycle (Fig. 4.1), 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. 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 are preferred). 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 recruitment. The recruits subsequently undergo harvest selection, completing the life cycle.

When modeling trait evolution, we assumed additive breeding values and an infinitesimal genetic model, such that trait values were determined by many genes of small effect, making heritability constant. The model did not consider effects of mutation. We also assumed a joint multivariate normal distribution for both breeding values and phenotypes (Lande & Arnold 1983). The model description below includes aspects of a recommended protocol for describing individual-based models (Grimm *et al.* 2006). The simulation code was primarily written in R v. 2.11.1 (R Development Core Team 2010), although the mating submodel was coded in Fortran 95 (Metcalf *et al.* 2004) and compiled using the freeware G95 compiler (http://www.g95.org/index.shtml).

State variables and scales

The model has two hierarchical levels: individuals and populations. 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 (years). Age is tracked as a discrete variable, with individual maturing at 3, 4, or 5 years of age. Unless otherwise stated (see Harvest Submodel), body length is defined as the linear measurement from the mideye 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 system (e.g. 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 overview and scheduling

Each simulation had individuals proceed through a sequence of stages occurring within the life history of sockeye salmon (Fig. 4.1). 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 years. 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: A Creek and A Beach, located in Little Togiak Lake in the Wood River Lakes system in southwestern Alaska (Lin *et al.* 2008a).

Phenotypic parameters were estimated from both populations, and quantitative genetic parameters (heritabilities for body length and body depth at maturity, genetic correlation between body length and body depth) were estimated using data from A Creek. The A Creek population has been sampled and characterized extensively from 2004 to present, which allowed us to reconstruct a one-generation molecular pedigree and estimate heritabilities and genetic correlations for body length, body depth, and age at maturity. In the A Creek and A Beach populations, almost all individuals mature at total ages of 3 to 5 years. We had body length and depth measurements for thousands of fish in A Creek and for hundreds of fish in A Beach, but only a subset of those data were associated with fish that had been aged by reading their otoliths. In A Creek, we had age, length, and depth data for 748 females and 321 males. For A Beach, we had data for 30 females and 12 males.

All available body length and depth data (for both aged and un-aged fish) were used to estimate means and standard deviations for age, body length and body depth for the model populations (Table 4.1). These values were used as inputs for initiating trait values in the simulated populations but did undergo some adjustments (see Model Calibration). The phenotypic data for the individuals with age data were used to estimate phenotypic variance-covariance matrices for age, body length, and body depth at maturity (Table 4.2). Trait variances within each population and each sex composed the diagonal elements of each matrix, and pairwise covariances between traits composed the off-diagonal elements.

Pedigree data from A Creek were used to estimate quantitative genetic parameters for the model (see Chapter 3 of this dissertation for more detailed methods). A Creek

individuals were genotyped at 11 DNA microsatellite markers for one generation, and a pedigree was reconstructed via maximum likelihood methods with the software program COLONY V. 2 (Jones & 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 an animal model and 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. 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 symmetrical, square matrix that describes the additive genetic variances of phenotypic traits and the genetic covariances between traits. For our model, $\boldsymbol{G} = h^2 * \boldsymbol{P}$, where ***P*** is a 7-trait phenotypic variance-covariance matrix. We calculated ***P*** based on empirical estimates of trait variances and covariances at age, resulting in a 7 by 7 matrix for each population that included body length at ages 3-5, body depth at ages 3-5, and continuous age at maturity. We assumed an h^2 value of 0.3, which was the smaller of the two heritability values estimated for body length and body depth at maturity using the animal model (see Chapter 3, this dissertation). The population-specific ***G*** matrices are shown in Table 3. 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.

One potential complication for predicting evolution is that the ***G*** matrix is expected to evolve over time in response to microevolution (Jones *et al.* 2003; Steppan *et al.* 2002). Assumptions of normality and a constant ***G*** are unlikely to be seriously violated when either the effective number of migrants ($N_e m$) or phenotypic differences between populations are small, but higher rates of gene flow may affect the shape and orientation of ***G*** (Guillaume & Whitlock 2007). However, there are currently no analytical methods for predicting how ***G*** will evolve in finite populations (Arnold *et al.* 2008), and we have therefore not modeled evolutionary changes 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 4.1) 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-off points were therefore created to separate fish into discrete age categories based on their continuous ages; for instance, if the age three-to-four cut-point was set at 3.5, an individual with a continuous age of 3.1 would be categorized as age three. These cut-points were initially set at 3.5 (age three-to-four) and 4.5 (age four-to-five) but were adjusted during model calibration (see below).

Because individuals mature at a variety of ages (3, 4, and 5), body lengths and body depths at different ages of maturity were back-calculated for each individual using linear equations with a stochastic component (mean=0 mm for body length and depth, variance=36 mm for body length, and variance=9 mm for body depth). Table 4.4 describes differences between traits at age used for the back-calculations, which were estimated using the empirical phenotypic data for fish that had been aged. Although the back-calculation method may not have been very accurate, the model was not particularly sensitive to initial morphological trait values, since trait values evolved and stabilized at different equilibrium values during the burn-in simulations.

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-off 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). The selected outputs were the means and variances of: 1) proportion of age 4 fish, 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-off 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 4.5.

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. 4.1).

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 system (Kendall & Quinn 2009). These studies suggest that the type and intensity of selection has varied over time and between sexes, but across all Nushagak populations, the fishery catches more males than females and more exploits populations with larger, older fish more heavily (Kendall *et al.* 2009). Size selectivity in 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 & Quinn 2009).

Forty-seven years of fisheries data (1963-2009) for the Wood River system were assembled and analyzed (N. Kendall and C. Cunningham, University of Washington School of Aquatic & Fishery Sciences (UW SAFS), pers. comm.). Catch data were separated by sex and grouped into 10mm 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:

Equation 1

$$P_{capture} = \alpha * \exp(-\frac{(fork\ length - \mu)^2}{2 * \sigma^2})$$

Parameter values were as follows: α = 0.55, μ = 533.0, σ = 122.2 for females, and α = 0.65, μ = 539.7, σ = 107.1 for males. Body lengths within the harvest submodel were defined as measurements from the mideye of the fish to the fork of the tail (fork lengths, 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 mideye-hypural lengths used in the rest of the model. Based on these harvest selectivity curves, 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 (Fig. 4.2).

Dispersal submodel

Dispersal was random with respect to fish phenotype. First, dispersal rates, defined as the proportion of a population that strayed to the other population, were set by the user. A cutoff value was selected to capture a comparable proportion of a random normal distribution with a mean of zero and standard deviation of one. For example, if the dispersal rate was set at 0.10, a cutoff value of -1.28 was chosen (equal to the inverse of the cumulative normal distribution for the specified rate). Each individual was then

assigned a random number drawn from that same distribution (mean=0, standard deviation = 1), and individuals with assigned values less than the cutoff were designated as dispersers.

Predation submodel

Bears are important agents of natural selection in streams (Quinn & Kinnison 1999; Ruggerone *et al.* 2000), removing approximately 12-96% of adults within each spawning population each year (Quinn *et al.* 2003, see also Chapter 3 of this dissertation). Prior research also suggests increased predation risk for fish with larger than average body sizes (Carlson & Quinn 2007; Quinn & Buck 2001) 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 system (C. Cunningham, UW SAFS, unpublished data). These data were separated by sex and grouped into 10mm body length bins, and the proportion of bear-killed fish was calculated for each bin.

Bear-killed individuals died before reproduction and therefore had zero fitness. However, in reality predation does not completely eliminate fitness because individuals may reproduce successfully before being killed. Comparisons of reproductive lifespans (days between stream entry and death) between bear-killed and senescent fish in C Creek, a Wood River stream similar in size to A Creek, indicated that the in-stream life span 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 (see Chapter 3 in this dissertation).

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 mideye-hypural body length (L) minus the body length of an individual with an expected predation probability of zero (L_{P0F} for females, L_{P0M} for males) as the independent variable. The following sex-specific predation models (see Fig. 4.3) were the result.

Equation 2

$$P_{predation,\ females} = 0.0013 * (L - L_{P0F})$$

$$P_{predation,\ males} = 0.0014 * (L - L_{P0M})$$

The predation submodel was not applied to the simulated beach-spawning populations, as risk of bear predation in beach habitat is generally considered negligible (Quinn *et al.* 2001b).

Mating submodel

The mating sub-model 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:

Equation 3

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

where x is the ratio of female to male body length, and a = 0.05, b = 0.95, β_0 = -10, β_1 = 10, and β_2 = 3 (Bromaghin *et al.* 2011). For a given female, a male was randomly selected

from all males 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 system (n=106, unpublished data but see 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 (Fig. 4.4) of the form:

Equation 4

$$fecundity = 11.54 * (L - L_{F0})$$

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, minimum fecundity was set at 2000 eggs, a value close to the lowest observed fecundity observed in our 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 rearing in freshwater and each year spent in the ocean. For

example, an individual that matured at four years of age had to survive the one year in freshwater and three years in the ocean, experiencing a total of four culls.

Total survival to recruitment was based on a re-parameterization 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 (number of individuals surviving to reproduce).

Equation 5

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

The parameter α controls the shape of the stock-recruitment relationship (population productivity), 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 Equation 5, 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:

Equation 6

$$\lambda_F = e^{\frac{-\alpha E}{\mu_F S_r}}$$

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. λ_{M1} was assumed equal for both sexes and randomly drawn each year from a log normal distribution with mean

Equation 7

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

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

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

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 (e.g. Rensel *et al.* 2010).

Heritability submodel

The heritability sub-model generated offspring phenotypes based on the concept that the variability of phenotypes (*X*) is the sum of a genetic (*G*) and environmental (*E*) component of variation (Roff 2010):

Equation 9

$$X = G + E$$

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 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 diagonal elements of the *G* matrix (Tufto 2010).

Equation 10

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

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 $\boldsymbol{R}$, where $\boldsymbol{R} = \boldsymbol{P} - \boldsymbol{G}$.

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).

Fitness submodel

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):

Equation 10

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

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 adaptive landscape (Simpson 1944) for the multiple traits represented in the population.

Conceptually, ω describes the curvature and orientation of a Gaussian fitness peak on the adaptive landscape. In terms of curvature, ω is analogous to the variance of a Gaussian distribution, such that a larger ω describes a wider, flatter peak with less curvature and hence weaker stabilizing selection (Arnold *et al.* 2001). Additionally, ω describes the orientation of the adaptive peak relative to the phenotypic character axes that define the adaptive 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. Together, these elements 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 & Whitlock 2007). When r_s is larger, the major axis of the adaptive peak is less parallel to the character axes (e.g. oriented at 45º in the phenotypic plane with the major axis increasing from left to right, assuming two traits that are positively correlated; see Fig. 3 in Arnold et al. 2001). This orientation 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 & Whitlock 2007).

We set the off-diagonal elements of ω to 25, a value used in prior studies to simulate mild stabilizing selection (Guillaume & Whitlock 2007; Jones *et al.* 2003). We then varied the strength of stabilizing selection by altering the diagonal elements of ω, such 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. An example of the effect of r_s on this fitness weight is depicted in Figure 1.3 (see Chapter 1 of this dissertation). 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 and validation

The model was tested by generating 200 individuals for each population and running them through the sequential stages in the model (Fig. 4.1). 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 years 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, μ = 533 for females and μ = 540 for males, Ricker productivity α = 2.25, replacement abundance (S_r) of the stream population = 3300, and S_r of the beach populations = 3000. Although the empirical census sizes for A Beach and A Creek are less than 1000 individuals each (see Chapter 3 of this dissertation), 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 years of the burn-in simulations (years 951-1000) were randomly grouped into ten blocks of data, with each block containing five years of recruits. Each data block was then used to initialize one of the ten replicates that were run for each simulation. Each simulation was run for 100 years.

The first set of simulations tested the evolutionary and demographic effects of the three submodels that applied selection to the simulated populations, namely the harvest submodel, the predation submodel, and the fitness submodel. 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, except that the bi-directional dispersal rate between populations was set as 0.025.

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 36 simulations that represented different combinations of stabilizing selection (four levels with r_s ranging from 0.25-1) and dispersal rates between populations (nine levels ranging from 0-0.2). Because the numbers of strays relative to the numbers of non-dispersers within a population ultimately determines the evolutionary effects of straying on that population, we show these ratios for each population at every simulated dispersal rate (Table 4.6). These ratios were calculated as the number of strays divided by the total number of individuals that spawned successfully (spawners). In the stream population, the number of strays was determined before predation selection occurred, whereas spawners had already experienced predation. To correct for this discrepancy, the number of strays was reduced by 21% (approximately the proportion of the stream population escapement removed by predation), to estimate the corrected proportion of strays (Table 4.6).

Model outputs were averaged over replicates for all simulations. The outputs we focused on specifically were: 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 years 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 $\boldsymbol{G}$), 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 model (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-year burn-in simulation with no dispersal between populations, equilibrium abundances (S_r) of 2000 individuals for each population, $h^2 = 0.3$, $r_s = 0.5$, $\mu = 533$ for females and $\mu = 540$ for males, and $\alpha = 2.25$. Each parameter was then independently varied (±10%) from the starting value used for the burn-in simulation, and the simulation was run for 100 years with a bi-directional dispersal rate of 0.025. For each simulation, ten replicates were run. 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 years had passed. Outputs were averaged across replicates, and the proportion of 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 years of the simulation (Fig. 4.5) and were consistent with the values attained during the 1000-year burn-in simulations. When predation selection on the stream population was removed, mean phenotypic trait values in that population changed only slightly (Fig. 4.6). In contrast, removing harvest selection caused a noticeable shift toward larger body sizes, especially in age-4 fish (Fig. 4.7). Even greater phenotypic changes were observed when stabilizing selection was removed, with decreased mean body sizes for each age class (Fig. 4.8), presumably because earlier maturation was favored by harvest selection. Evolution of early maturation was also observed in age structure; the proportion of age-3 individuals increased from about 2% to 95% in the stream population, and from 0.5% to 87% in the beach population after 100 years. Consequently, the overall mean trait values within each population were very low, around 300mm for body length and 80mm for body depth. These results are consistent with the expectation that harvest size selectivity was greater in the stream than in the beach population (Fig. 4.2).

Removing the harvest and fitness submodels also had the greatest demographic impacts relative to the baseline scenario. When no harvest occurred, mean spawner number increased 65% within the stream population and 83% in the beach population

(Fig. 4.9). Removing stabilizing selection had similar demographic effects, although the increase in spawner number in the beach population was noticeably lower (71%; Fig. 4.9). The demographic effect of removing predation was comparatively small, resulting in a spawner increase of about 17% in the stream population (Fig. 4.9). Examining the total run sizes (number of individuals surviving freshwater and marine juvenile stages but before harvest) and escapements (number of returning fish that escaped harvest) revealed some additional information about the effects of stabilizing selection on demography. Specifically, removal of stabilizing selection led to evolution of smaller body sizes that made the salmon less susceptible to the fishery. For example, with stabilizing selection, harvest removed 56% of returning stream fish and 70% of returning beach fish. Without stabilizing selection, harvest removed 19% of returning stream fish and 23% of returning beach fish. Under both scenarios, larger-bodied beach spawners were more susceptible to harvest than smaller-bodied stream spawners.

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. Dispersal rates were similar to the proportion of strays within each population (Table 4.6), and thus the potential evolutionary impact of dispersal should be closely tied to dispersal rate. When examining morphology, we focused on the trait of male body depth since it was the trait that showed the most differentiation between ecotypes. Both harvest selection ($\mu = 533$ for females and $\mu = 540$ for males) and predation selection were included in these simulations. Harvest rates removed approximately 40-76% of recruits from each population each year (see Equation 1 for the model), whereas predation

removed about 20-30% of individuals returning to the stream population each year (see Equation 2).

For this set of experiments, we varied dispersal rates and intensity of stabilizing selection. Varying stabilizing selection alone (no dispersal applied) showed that mean male body depth increased with stabilizing selection in both populations (Fig. 4.10). Varying dispersal rates alone (with r_s constant at 0.5) demonstrated that increasing dispersal caused body depths to increase in the stream population and decrease in the beach population (Fig. 4.11), making the two populations more phenotypically similar. In terms of age structure, the proportion of age-4 individuals within each population (both sexes) increased with stabilizing selection, whereas proportions of age-3 fish decreased (Fig. 4.12. Proportions of age-5 fish were highest at intermediate levels of stabilizing selection (Fig. 4.13). When dispersal rates increased, the proportion of age-5 individuals increased slightly in the stream population and decreased slightly in the beach population (Fig. 4.12), again demonstrating the homogenizing effects of gene flow.

As expected, stabilizing selection 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. Interestingly, 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.

4.14). However, these patterns do not relate directly to local adaptation within each population, which always increased with stabilizing selection.

Stabilizing selection also had greater effects on demography than did dispersal at the rates considered (0-0.2), with spawner numbers decreasing in both populations as stabilizing selection increased (Fig. 4.15). This was due to the fact that fish phenotypes favored under stabilizing selection were more vulnerable to harvest selection, which resulted in smaller population sizes when stabilizing selection was high. Recruits per spawner increased with stabilizing selection (Fig. 4.16), because the salmon were closer to their population optima and had higher fitness. Density dependence may have also increased the number of recruits per spawner because overall spawner numbers were lower (Fig. 4.15). Indeed, overall population growth rates over time were constant for both populations (Fig. 4.17). The differences due to stabilizing selection were more pronounced in stream spawners than in beach spawners.

Dispersal impacted population sizes to some extent, with the effects differing between ecotypes. As dispersal rate increased, stream spawner numbers decreased slightly, whereas beach spawner numbers increased slightly (assuming constant stabilizing selection; Fig. 4.18). There were two reasons for this pattern, one evolutionary and one demographic. First, increasing dispersal caused stream fish to become larger and beach fish to become smaller, except when stabilizing selection was very strong. Thus when dispersal rate increased, stream fish were more susceptible to the fishery, whereas beach fish were less susceptible. Second, with $r_s > 0.25$ and increasing dispersal rate, the number of dispersers moving from the stream to the beach population increased relative to the number moving in the opposite direction. The discrepancy in the number of

dispersers was small, however (maximum discrepancy of 115 individuals), and insufficient to completely explain the trends observed with varying dispersal.

Under the parameter values simulated, dispersal did not appear to impact population productivity by affecting local adaptation. Local adaptation increased with stabilizing selection, as non-dispersing individuals had higher reproductive success, especially in males (Fig. 4.19). Nevertheless, within each level of stabilizing selection, individual reproductive success stayed fairly constant with changing dispersal rates (Fig. 4.19). Calculations of relative reproductive success (mean individual reproductive success of immigrants divided by mean individual reproductive success of non-dispersers) indicated that immigrants generally had decreasing reproductive success as stabilizing selection increased (Fig. 4.20), a pattern that was more pronounced in males because male ecotypes differed more in body size than did female ecotypes. Overall, the results suggested that dispersal had relatively small impacts on population sizes, whether through direct immigration or impacts on local adaptation.

Sensitivity analysis

Sensitivity analysis revealed that, of the tested parameters, μ (length of peak vulnerability to harvest selection) had the greatest effect on mean trait values within populations. Patterns for body length and body depth were very similar; increasing μ by 10% increased mean trait values in stream males while slightly decreasing mean trait values in beach males (Fig. 4.21). Decreasing μ by 10% led to larger body sizes in both stream and beach populations, with a higher proportion of change in the stream population (Fig. 4.21). Increasing μ had little impact on the proportion of age-5 fish in either population, but decreasing μ increased the proportion of age-5 individuals in the

stream population and decreased the proportion of age-5 individuals in the beach population (Fig. 4.22). These changes arose because increasing μ allowed relatively large stream males to escape the fishery while simultaneously causing a larger proportion of relatively large beach spawners to be caught. Conversely, decreasing μ caused smaller fish within both populations to be caught, with body size selectivity being greater in the stream population (Fig. 4.21). Because these smaller fish were caught, more age-5 fish persisted in both the stream and beach populations. In contrast, varying heritability (h^2) and productivity (α) had comparatively smaller effects on phenotypic divergence (Figs. 4.21 and 4.22).

The parameter μ also had the largest impact on the mean number of spawners, more so in the stream population than the beach population. Increasing μ resulted in larger spawner numbers in both populations (Fig. 4.23) because fewer of the individuals were vulnerable to the fishery, especially in the stream population. 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 increased because beach spawners were less likely to be caught (Fig. 4.23). Increasing α also increased spawner numbers, but changing h^2 had relatively little impact on population sizes (Fig. 4.23). Changing μ had almost the opposite effects on recruits per spawner (Fig. 4.24), likely due to the density dependence implemented in the model. When the number of spawners increased, there was a decline in the number of recruits that each spawner produced.

Discussion

Here we developed an individual-based, quantitative genetic model to simulate trait evolution and population dynamics in connected populations of 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 harvest selection and stabilizing selection 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 sizes, 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 could be due to two reasons. First, younger ages, and consequently smaller sizes, may be favored because fish will have increased fitness if they reproduce before being caught (Dieckmann & 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 (Fig. 4.21). 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 & Quinn 2009). Thus, the evolutionary effects of the harvest submodel on body size appeared 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. 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 an independent force; rather, it results from opposing selective forces on a trait, such as temporal variability in selection (Madsen & Shine 1993) or interactions between sexual selection and predation selection (see Chapter 3 of this dissertation). The finding that stabilizing selection was required to maintain reasonably large fish body sizes suggests that our selection models may need adjustment, or that there are selective forces operating in nature we did not identify. 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).

Another important result was that the interaction between stabilizing selection and harvest selection affected population dynamics. Increasing stabilizing selection led to the evolution of phenotypes that were more susceptible to harvest, decreasing equilibrium population sizes (Fig. 4.13). Although recruits per spawner increased with stabilizing selection (Fig. 4.16), population growth rates stayed constant (Fig. 4.15) and did not completely counter the demographic effects of increased vulnerability to harvest. There is increasing concern about evolutionary change affecting population dynamics (Hutchings & Fraser 2008; Saccheri & Hanski 2006), and our model shows how conflicting selection pressures might have a pronounced effect on demography within 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 may apply to iteroparous and terrestrial species as well, because harvest selection should also select for smaller body sizes in these species, and because multiple episodes of selection on the same cohort may produce a strong response to selection (Eldridge *et al.* 2010)

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 negative effects on productivity 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 somewhat minimized. There was also sufficient phenotypic diversity in the offspring of immigrant parents that some always survived stabilizing selection. Thus, retaining 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 changes (Hard *et al.* 2008).

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 (Fig. 4.14). However, under higher dispersal rates ($m > 0.05$), stabilizing selection had a greater impact on phenotypic differentiation (Fig. 4.14). 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. Regardless, under all investigated scenarios, increasing dispersal resulted in reduced local adaptation.

Although the model does provide some interesting results regarding the effects of selection on body size, there are some model components that could use additional refinement. For example, differences in body size between age-4 and age-5 fish were sometimes very small (e.g. Fig. 4.6), 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 (Fig. 4.12), 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 have a better understanding of the selection pressures that operate in nature.

Because the model is designed to be very flexible, we would eventually like to use it for testing other hypotheses. For instance, we would like to determine how phenotype-biased dispersal may affect local adaptation, as previous research has found evidence for this phenomenon in sockeye salmon (Lin *et al.* 2008a). In theory, adaptive divergence will increase when there is selection against phenotypically distinct immigrants (Garant *et al.* 2007; Hendry 2004), but variation in selection intensity as well as the phenotypes of potential immigrants may affect 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 & Hill 2008). In sockeye salmon specifically, fishery selection differentials vary temporally (Kendall *et al.* 2009), which may have different evolutionary consequences than consistent selection for a specific and narrow range of body sizes.

In conclusion, the model simulated evolution of correlated phenotypic traits affecting reproductive fitness in 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. Although we did not observe strong direct impacts of gene flow on reduction of population productivity, the model did demonstrate that evolutionary change can have demographic consequences over ecologically relevant time scales. We intend to extend the model

further and believe it may serve as a useful tool for linking population genetics to population dynamics.

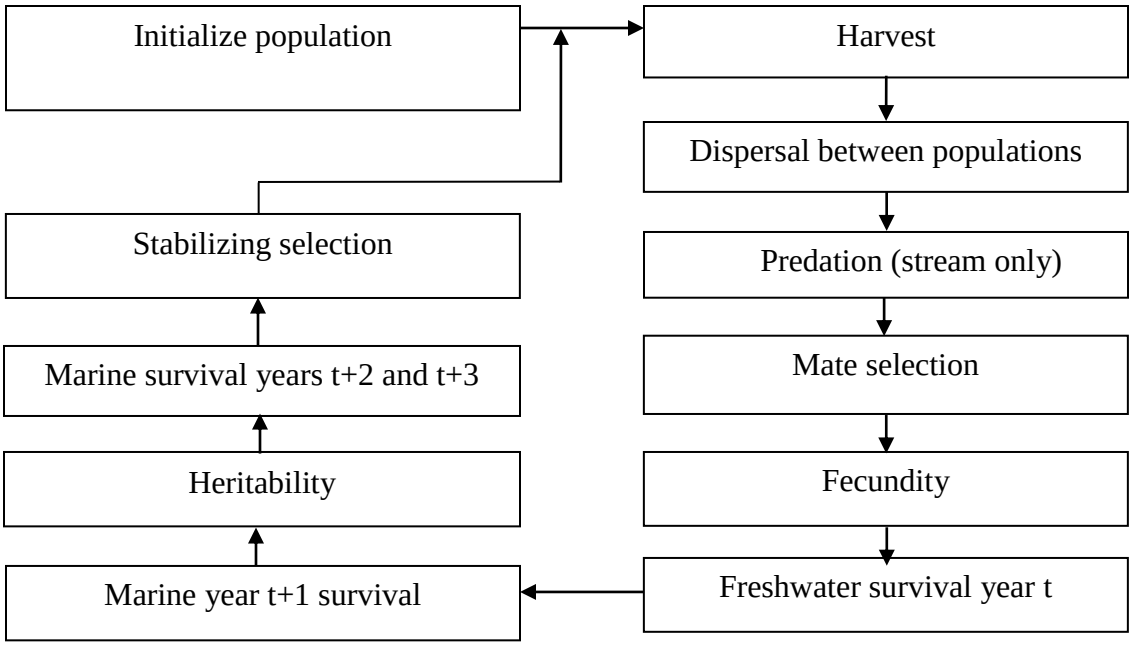


Figure 4.1. Flowchart of simulation model processes.

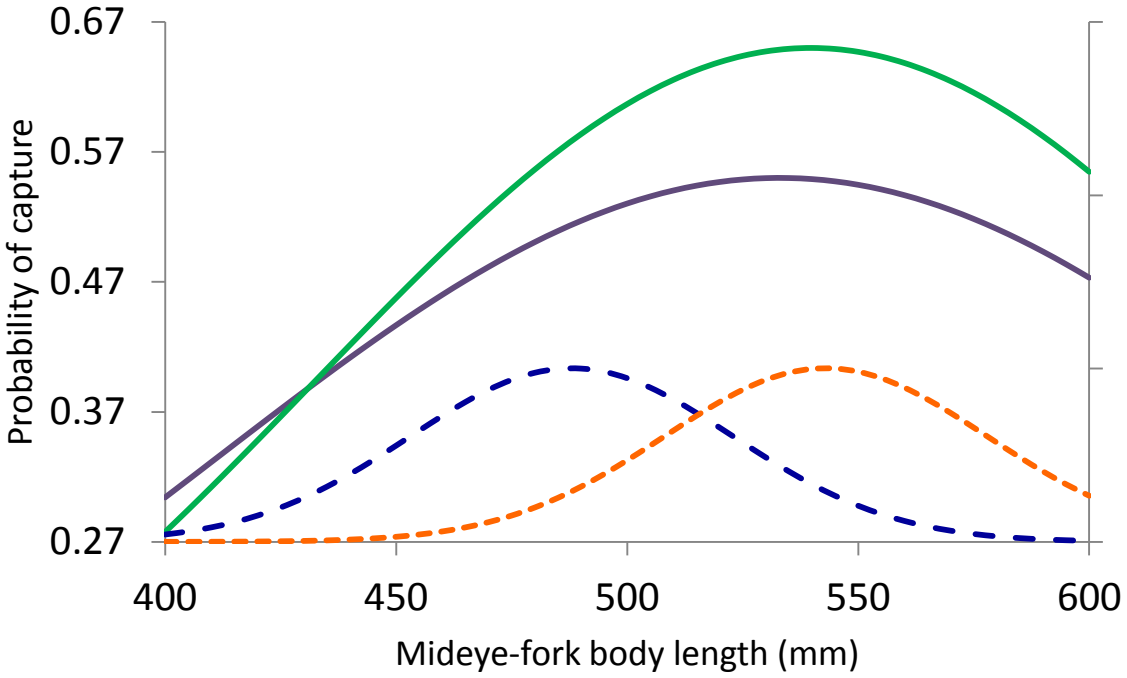


Figure 4.2. Harvest selectivity curves on mideye-fork body length (males in green, females in purple) compared to the distributions of optimal mideye-fork male body lengths in the stream population (blue dashed line) and beach population (orange dotted line). These curves show that harvest selectivity for smaller body size will be stronger in the stream than the beach population, because the larger individuals within the stream population are substantially more vulnerable to harvest than the smaller individuals within the population.

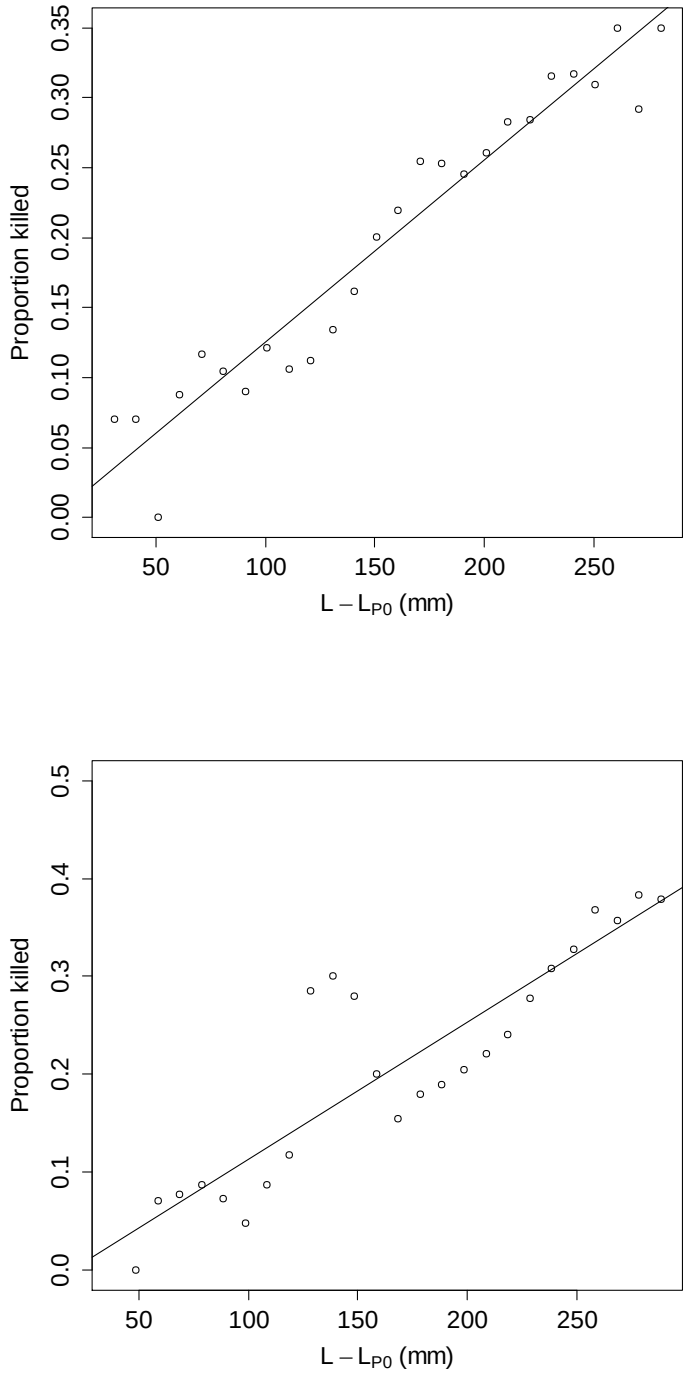


Figure 4.3. Linear predation selection models for females (top) and males (bottom), based on the difference between body length (L) and the body length at which the expected predation probability is zero (L_{P0}). For the female model, $r^2 = 0.93$, and for the male model, $r^2 = 0.76$. Data were obtained from the Hansen Creek population.

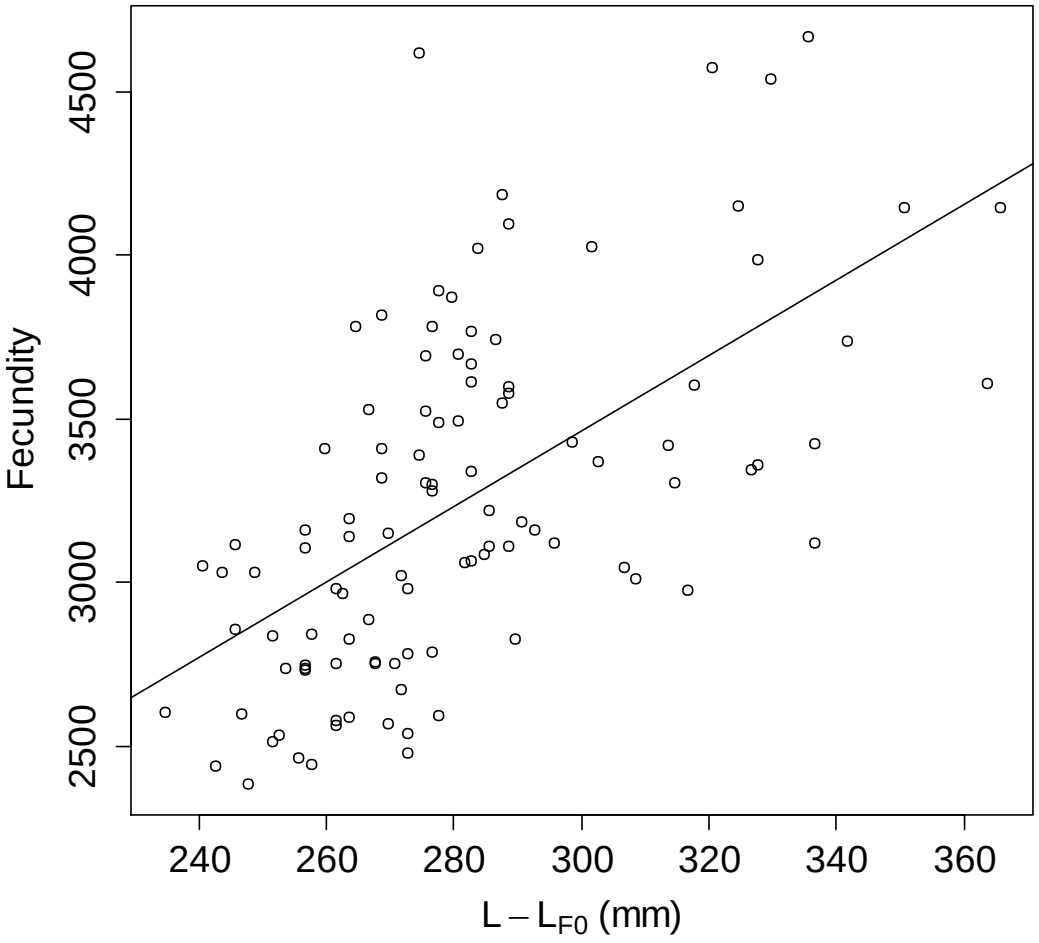


Figure 4.4. Linear model for fecundity based on the difference between body length (L) and the body length at which the expected fecundity is zero (L_{F0}, $r^2 = 0.35$).

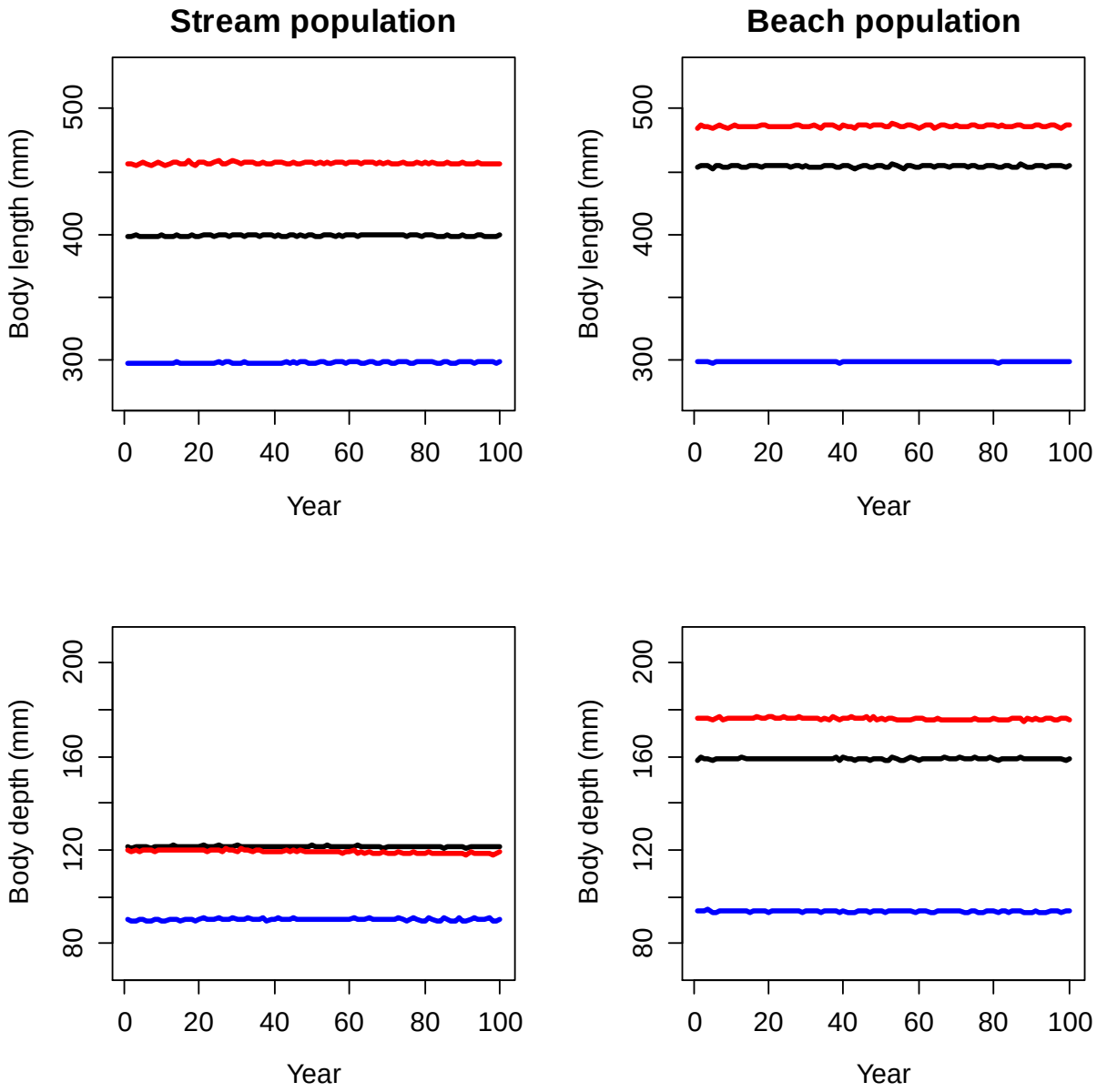


Figure 4.5. Mean body length (top) and body depth (bottom) over time in the stream and beach populations, for each age class in males. Age-3 means are in blue, age-4 means in black, and age-5 means in red. Here the baseline simulation parameters including all selection submodels were used.

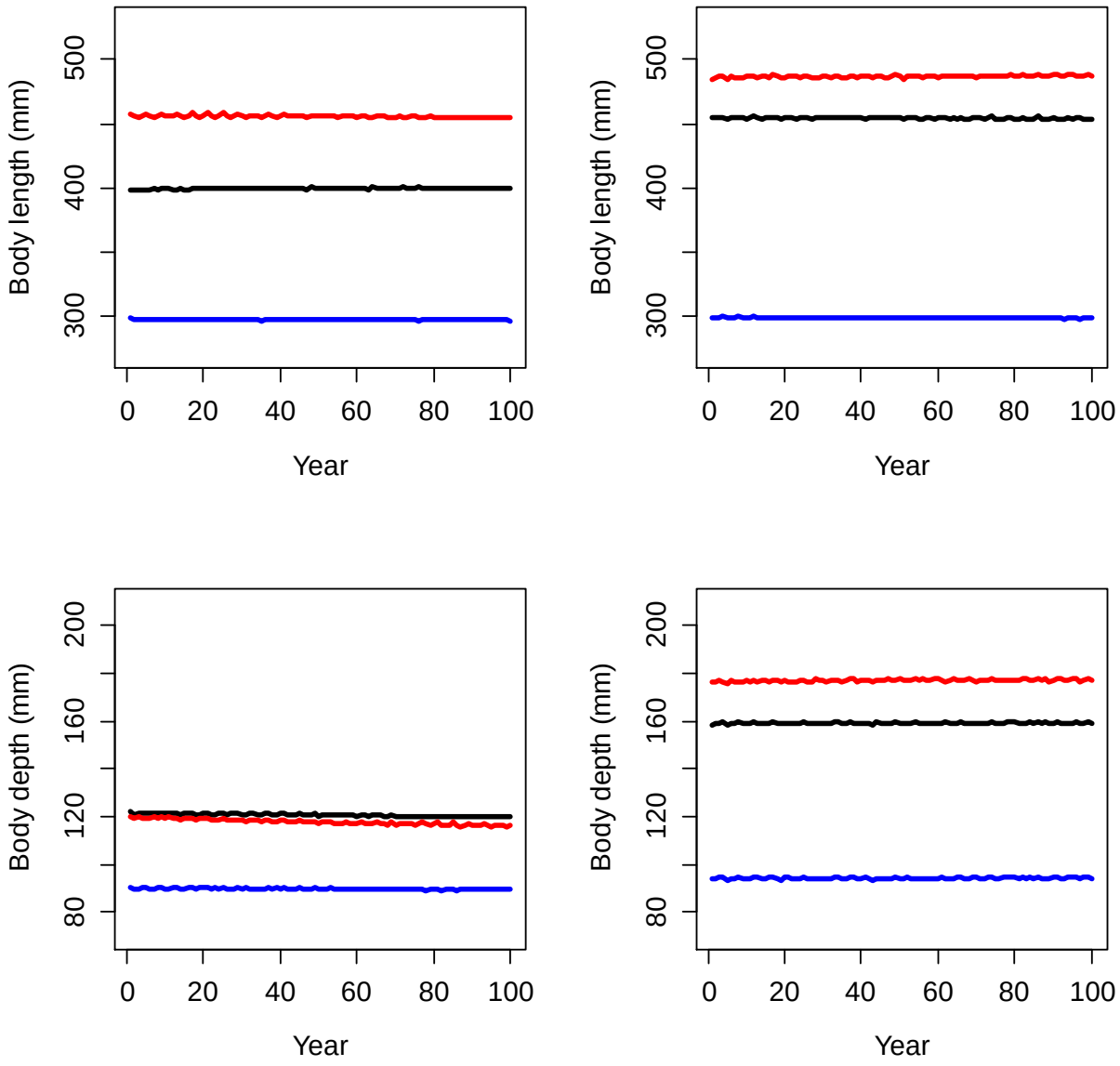


Figure 4.6. Mean body length (top) and body depth (bottom) over time in the stream and beach populations, for each age class in males. Age-3 means are in blue, age-4 means in black, and age-5 means in red. Here no predation selection was applied.

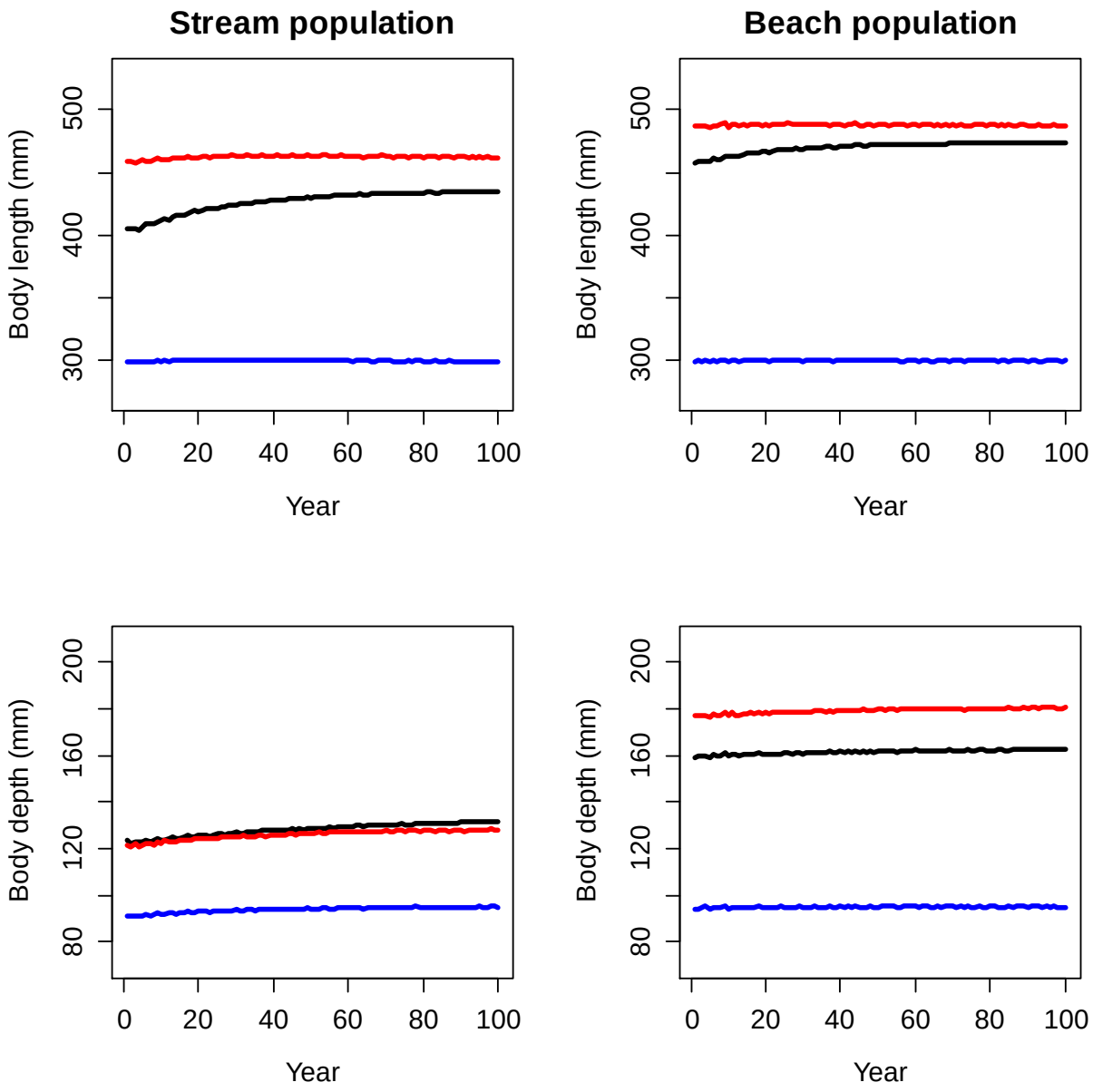


Figure 4.7. Mean body length (top) and body depth (bottom) over time in the stream and beach populations, for each age class in males. Age-3 means are in blue, age-4 means in black, and age-5 means in red. Here, no harvest selection was applied.

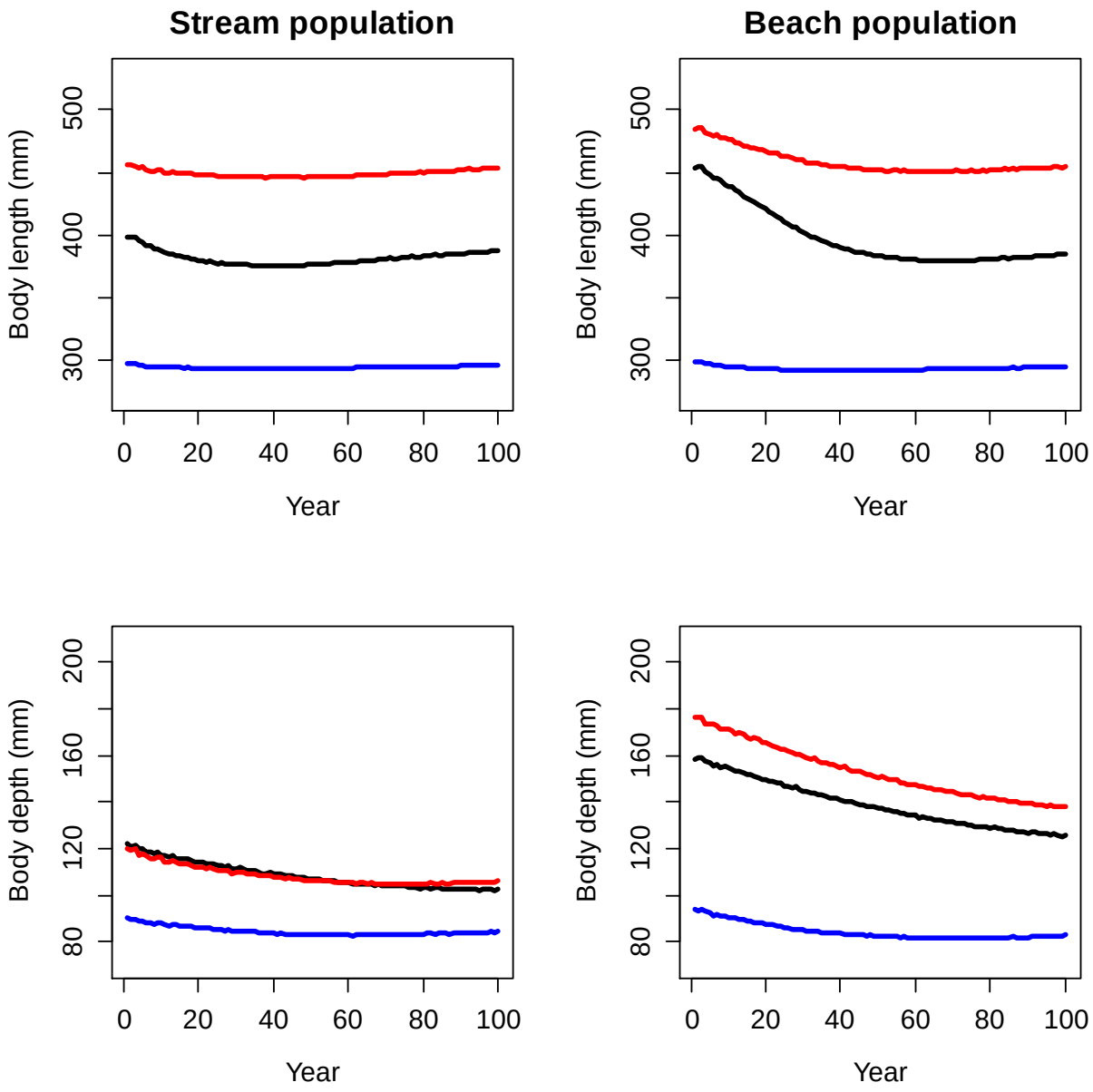


Figure 4.8. Mean body length (top) and body depth (bottom) over time in the stream and beach populations, for each age class in males. Age-3 means are in blue, age-4 means in black, and age-5 means in red. Here, no stabilizing selection within populations was applied.

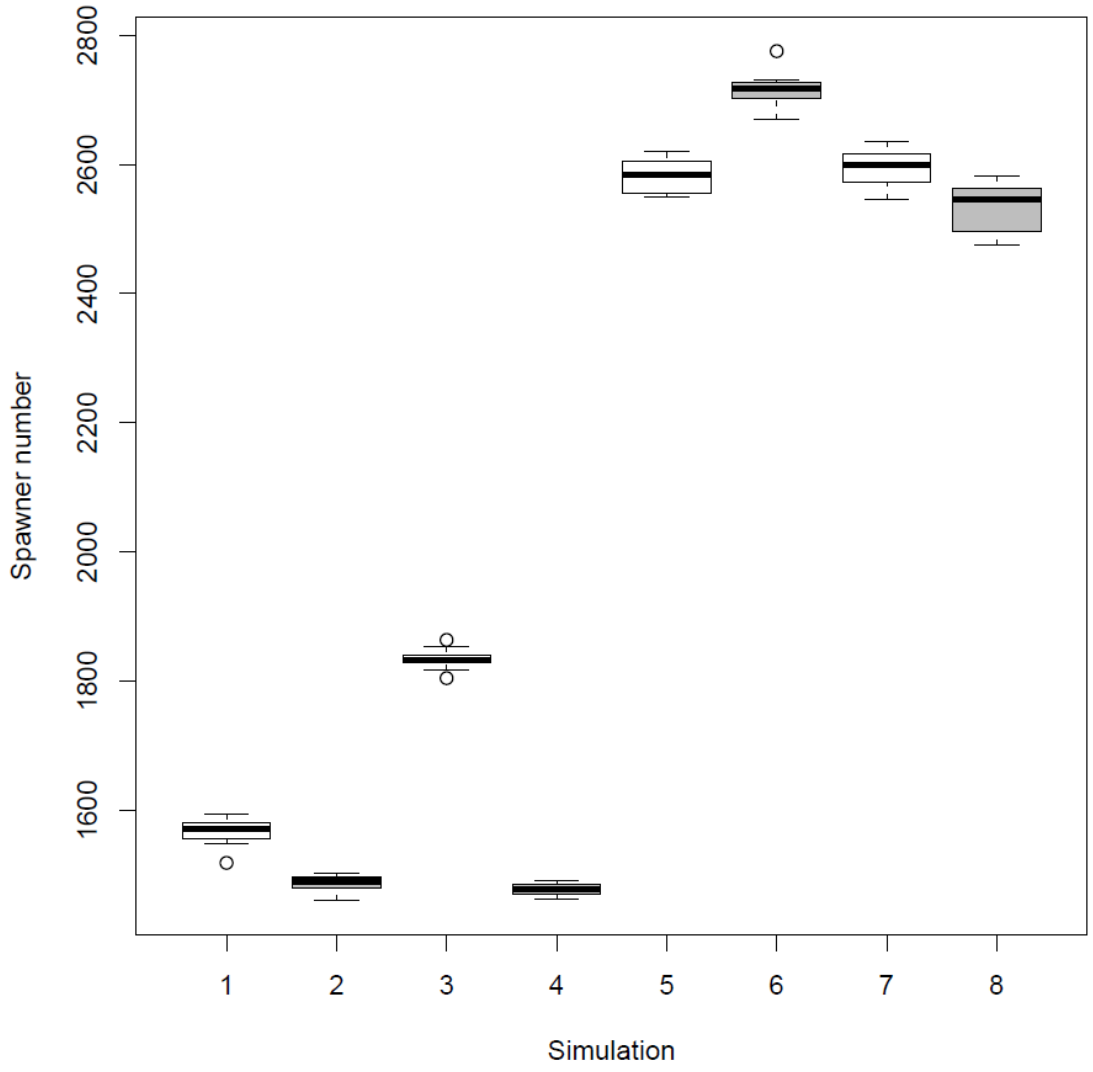


Figure 4.9. Boxplots of mean spawner number for the simulations where different selection submodels were removed. The data consist of mean spawner number over the 100 years of each simulation, and variation in the mean over replicates. Simulations 1 and 2 included all selection submodels, 3 and 4 had predation selection removed, 5 and 6 had harvest selection removed, and 7 and 8 had stabilizing selection removed removed. Data for the stream population are in white (odd simulation numbers), and data for the beach population are in grey (even simulation numbers).

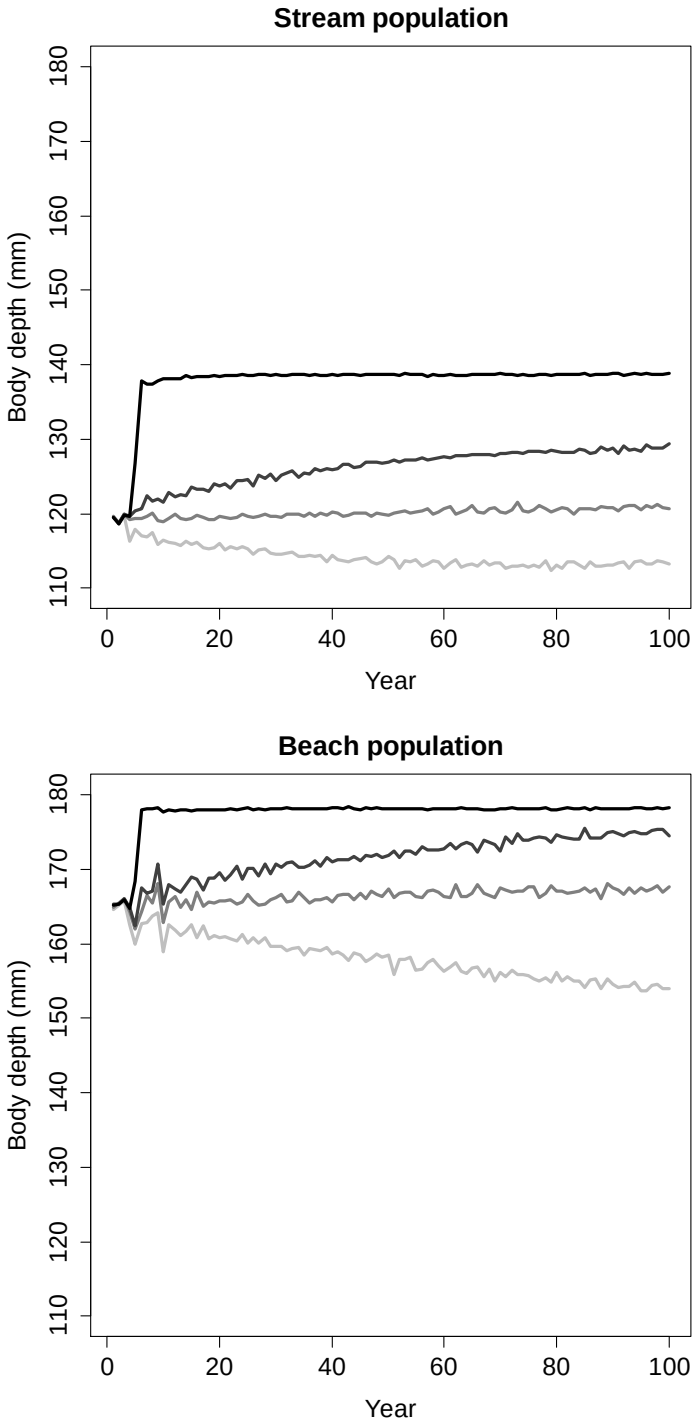


Figure 4.10. Changes in male body depth in the stream (top) and beach population (bottom) at varying levels of stabilizing selection (r_s = 0.25, 0.50, 0.75, 1.0), with no dispersal between populations. The darker the line, the higher the value of r_s.

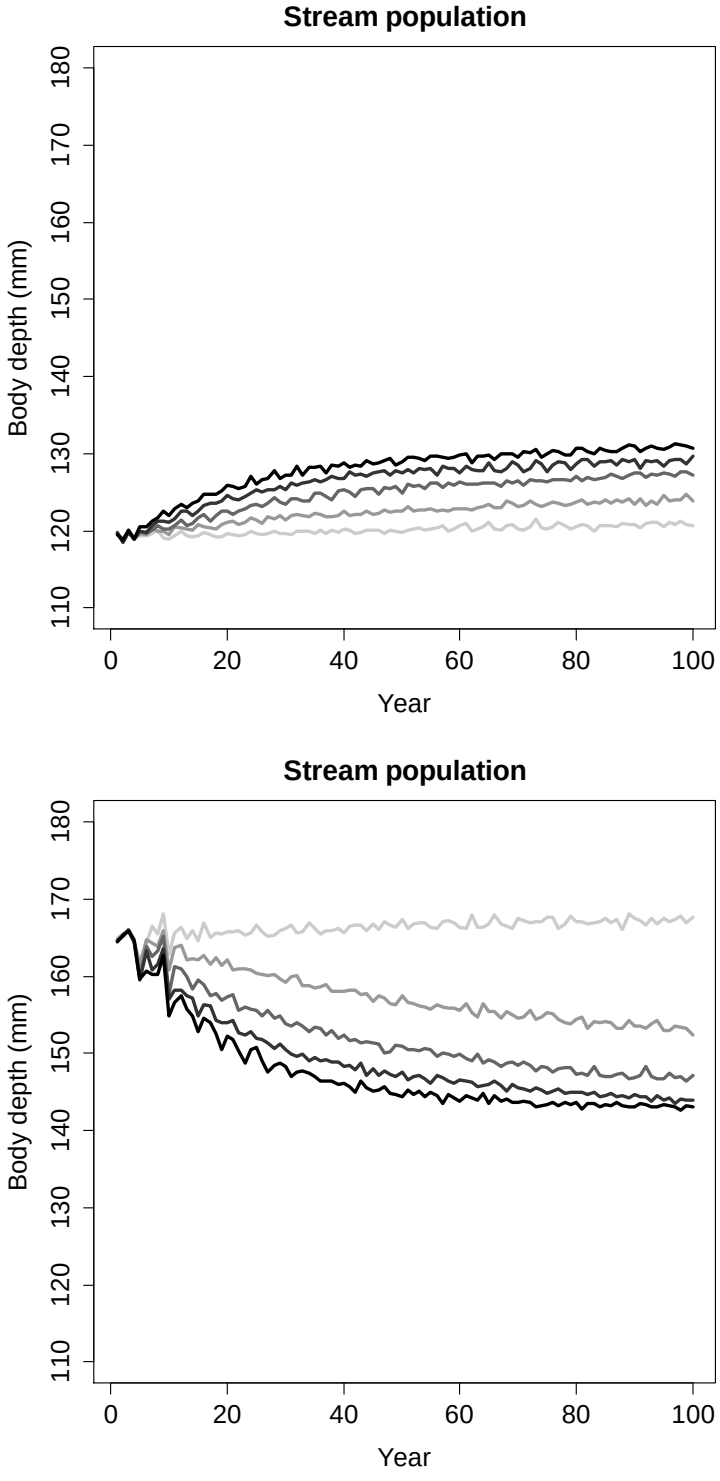


Figure 4.11. Changes in male body depth in the stream (top) and beach population (bottom) at varying dispersal rates (m = 0, 0.05, 0.10, 0.15 and 0.20) under a constant level of stabilizing selection (r_s = 0.50). The darker the line, the higher the dispersal rate.

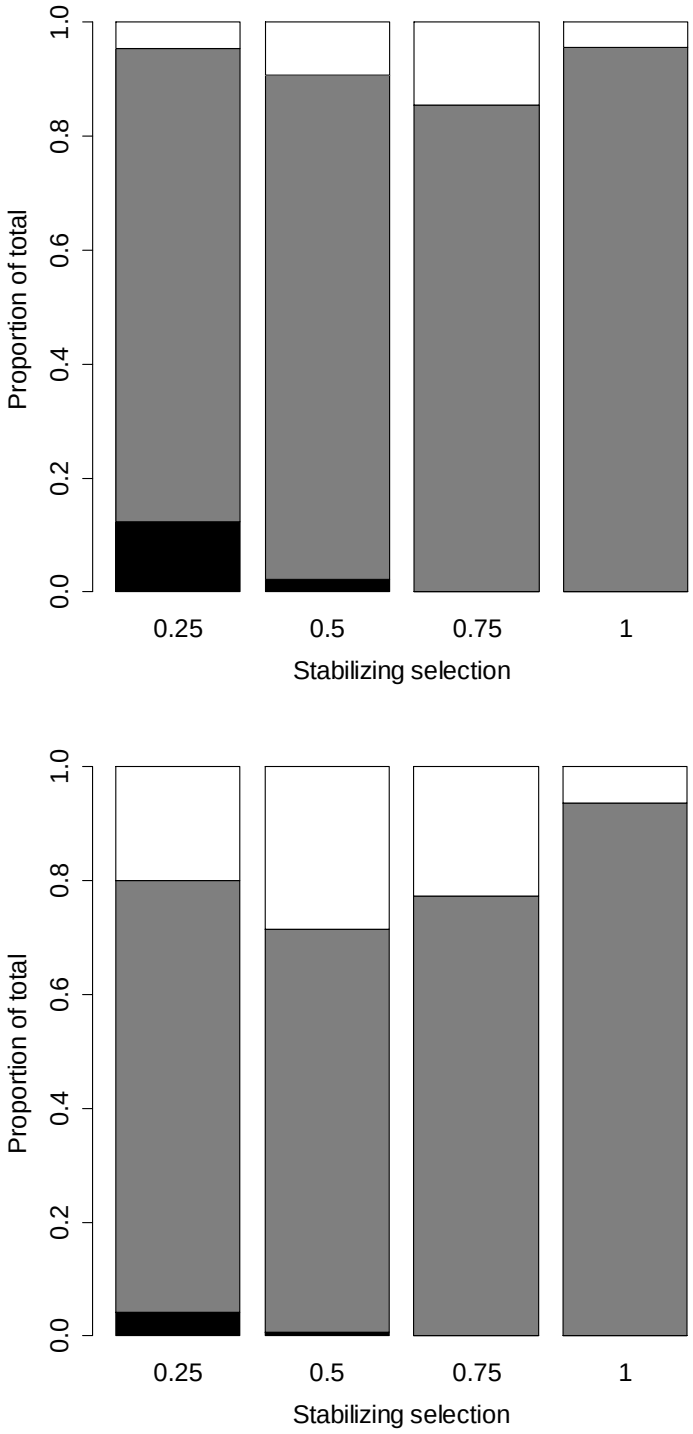


Figure 4.12. Changes in age structure at varying levels of stabilizing selection (r_s) and no dispersal, with data from the stream population on top and data from the beach population on the bottom. The proportion of individuals that matured at age-3 is in black, age-4 in grey, and age-5 in white.

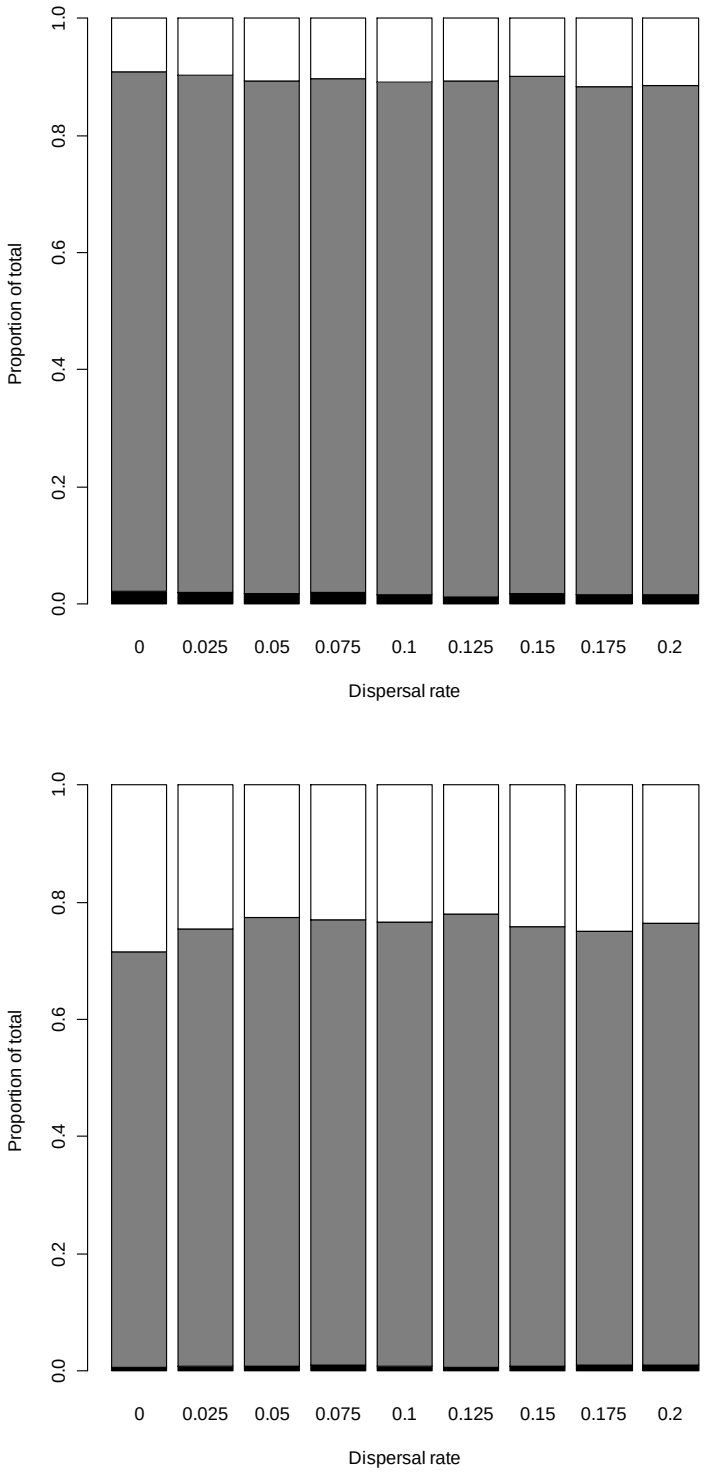


Figure 4.13. Changes in age structure at varying dispersal rates and constant stabilizing selection ($r_s = 0.5$), with data from the stream population on top and data from the beach population on the bottom. The proportion of individuals that matured at age-3 is in black, age-4 in grey, and age-5 in white.

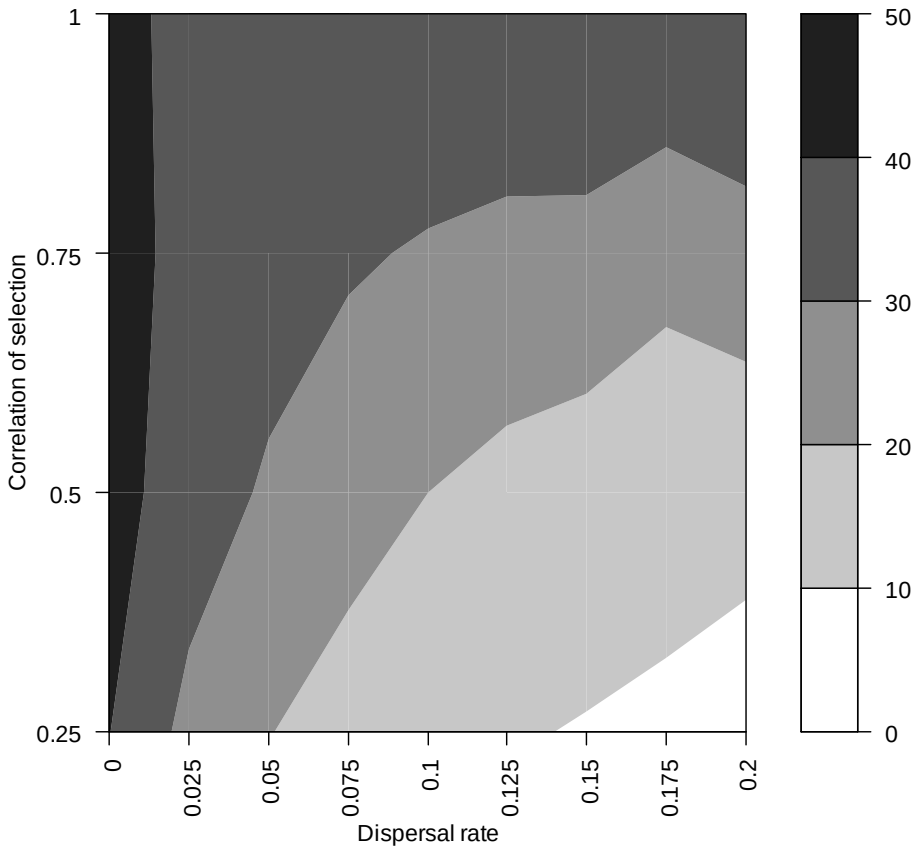


Figure 4.14. Contour plot of differences in male body depth at maturity (mm) between the two populations, after 100 years. The correlation of selection on body length and depth is unitless and relates to the strength of stabilizing selection, and dispersal rate corresponds to the proportion of individuals within each population that disperse.

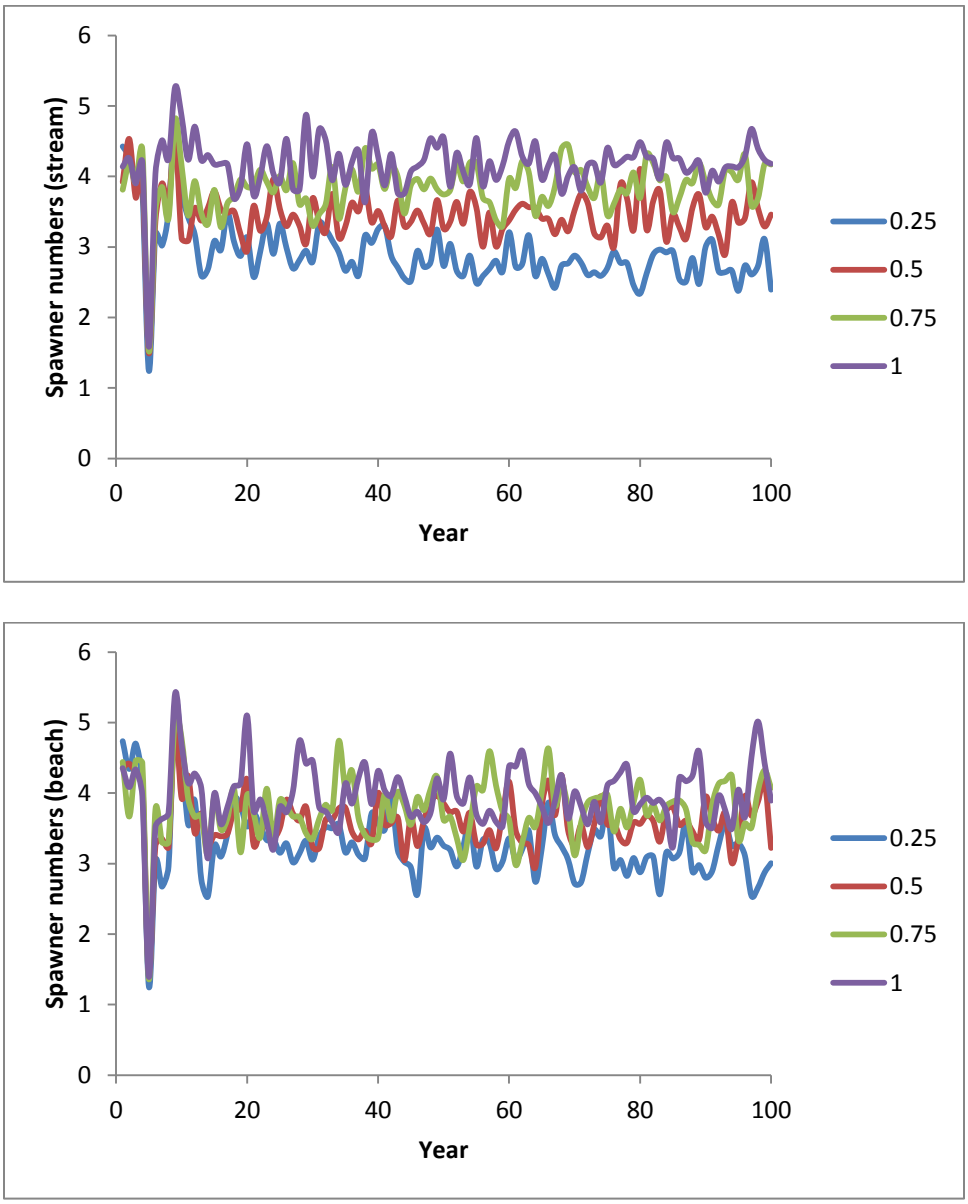


Figure 4.15. Spawner numbers over time in the stream (top) and beach (bottom) populations. These simulations did not include dispersal and show variation over levels of stabilizing selection (r_s; 0.25 = blue, 0.50 = red, 0.75 = green, 1.00 = purple).

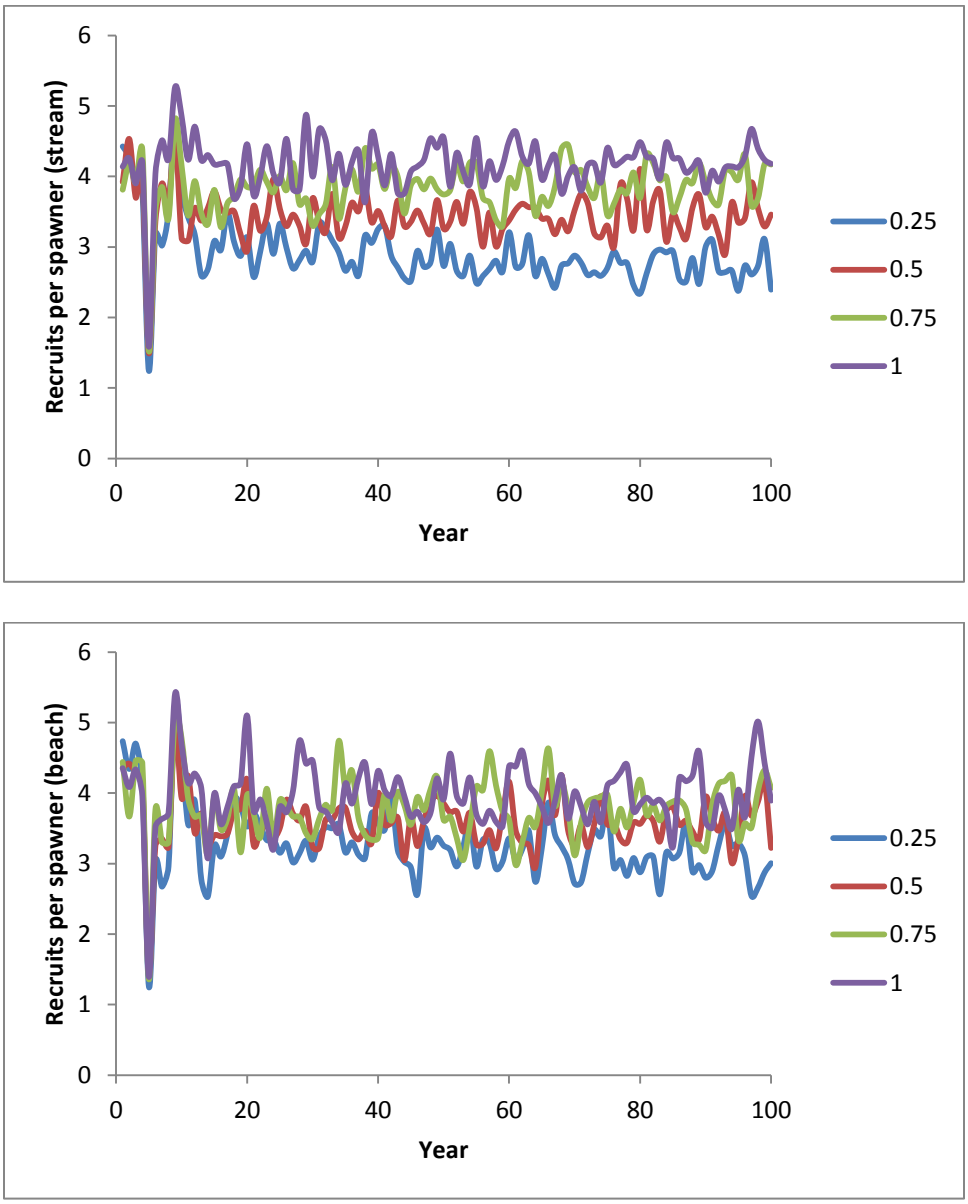


Figure 4.16. Recruits per spawner over time in the stream (top) and beach (bottom) populations. These simulations did not include dispersal and show variation over levels of stabilizing selection (r_s; 0.25 = blue, 0.50 = red, 0.75 = green, 1.00 = purple).

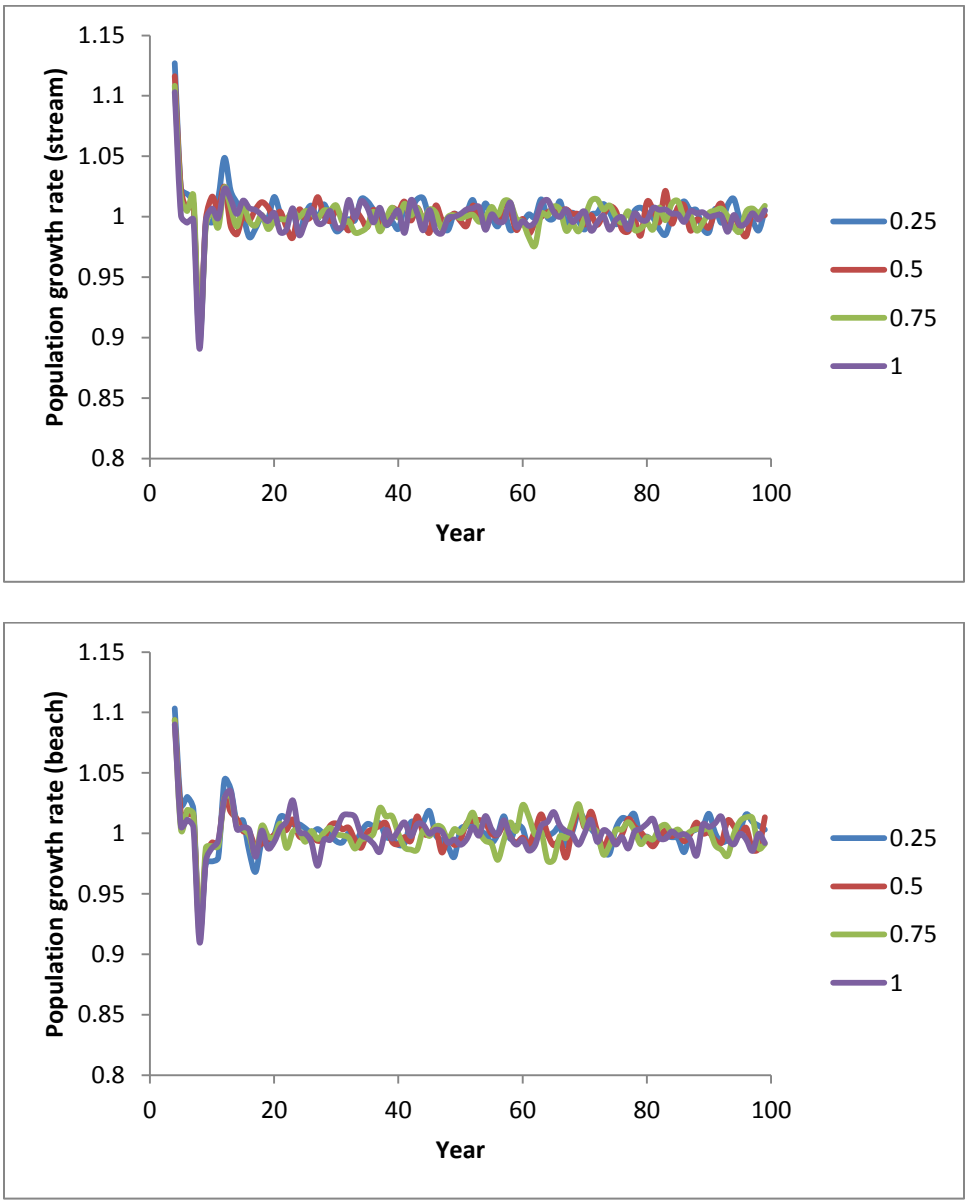


Figure 4.17. Population growth rates over time in the stream (top) and beach (bottom) populations. These simulations did not include dispersal and show variation over levels of stabilizing selection (r_s; 0.25 = blue, 0.50 = red, 0.75 = green, 1.00 = purple).

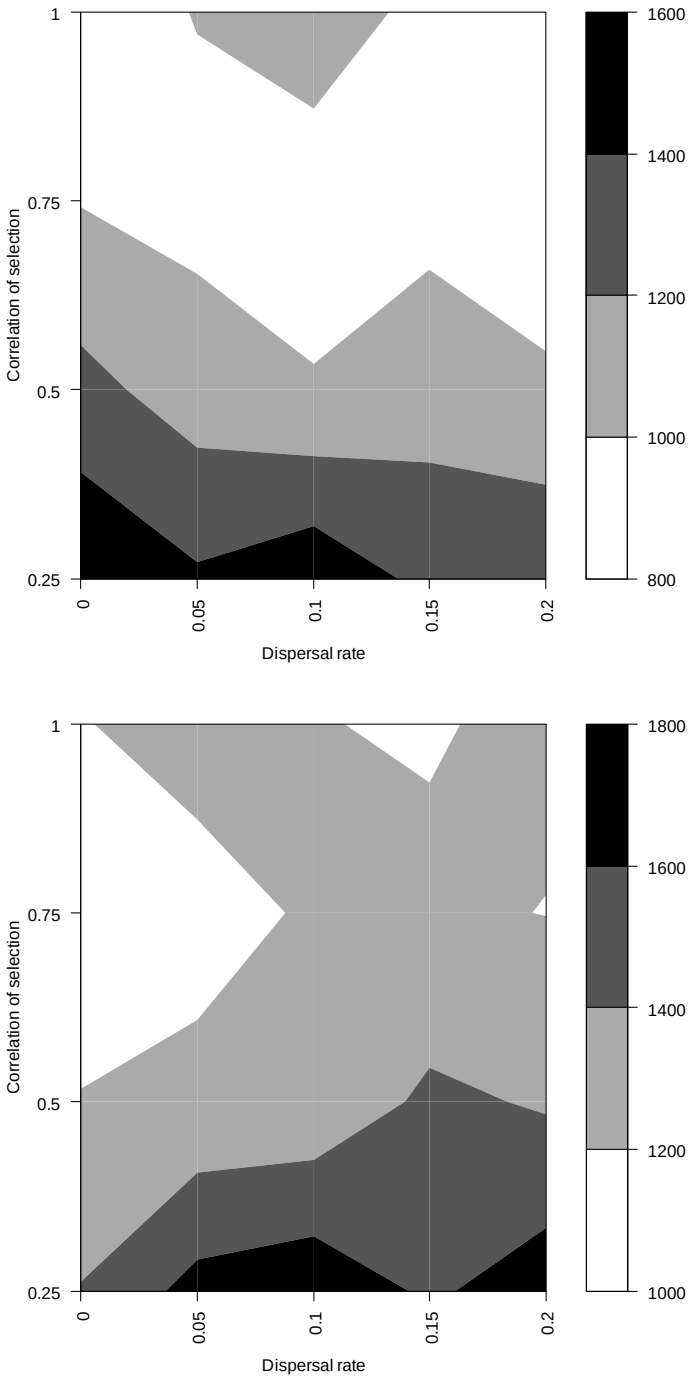


Figure 4.18. Contour plots of mean spawner numbers after 100 years, with darker colors corresponding to a greater spawner number. Data for the stream population are on top, and data for the beach population are on the bottom. The correlation of selection on body length and depth is unitless and is positively related to the strength of stabilizing selection, and dispersal rate corresponds to the proportion of individuals within each population that disperse.

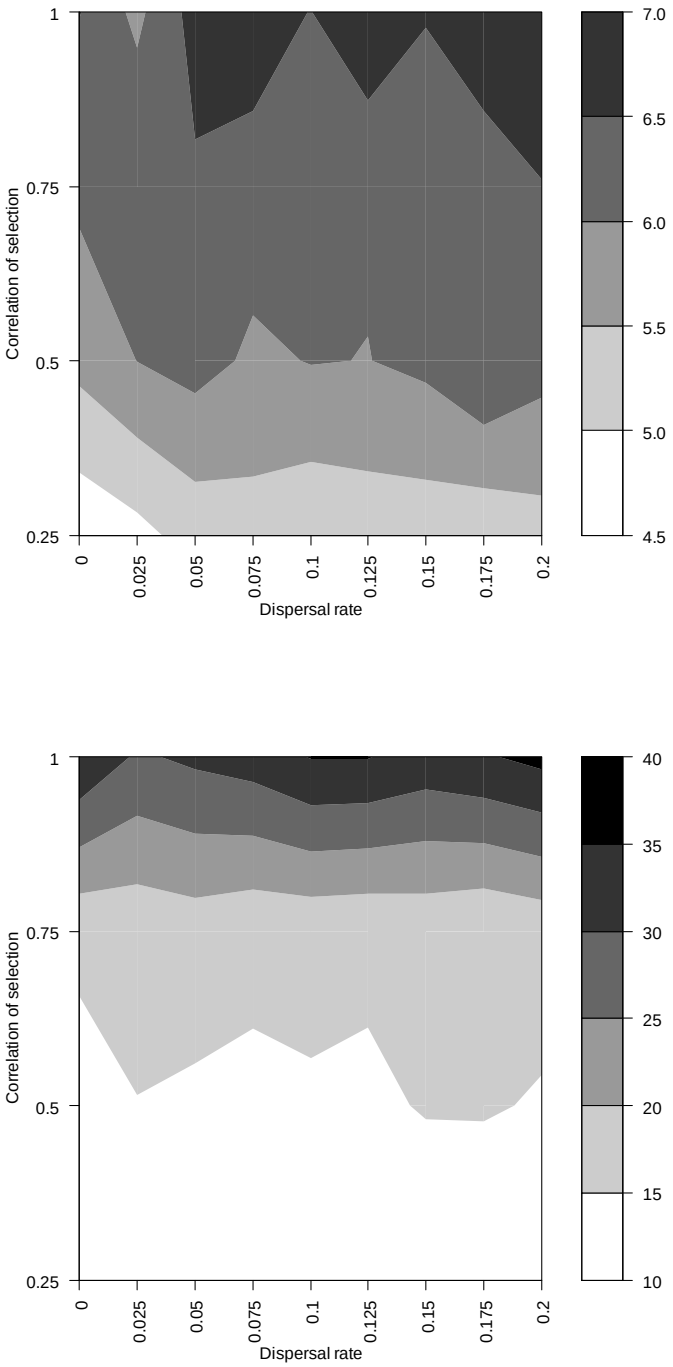
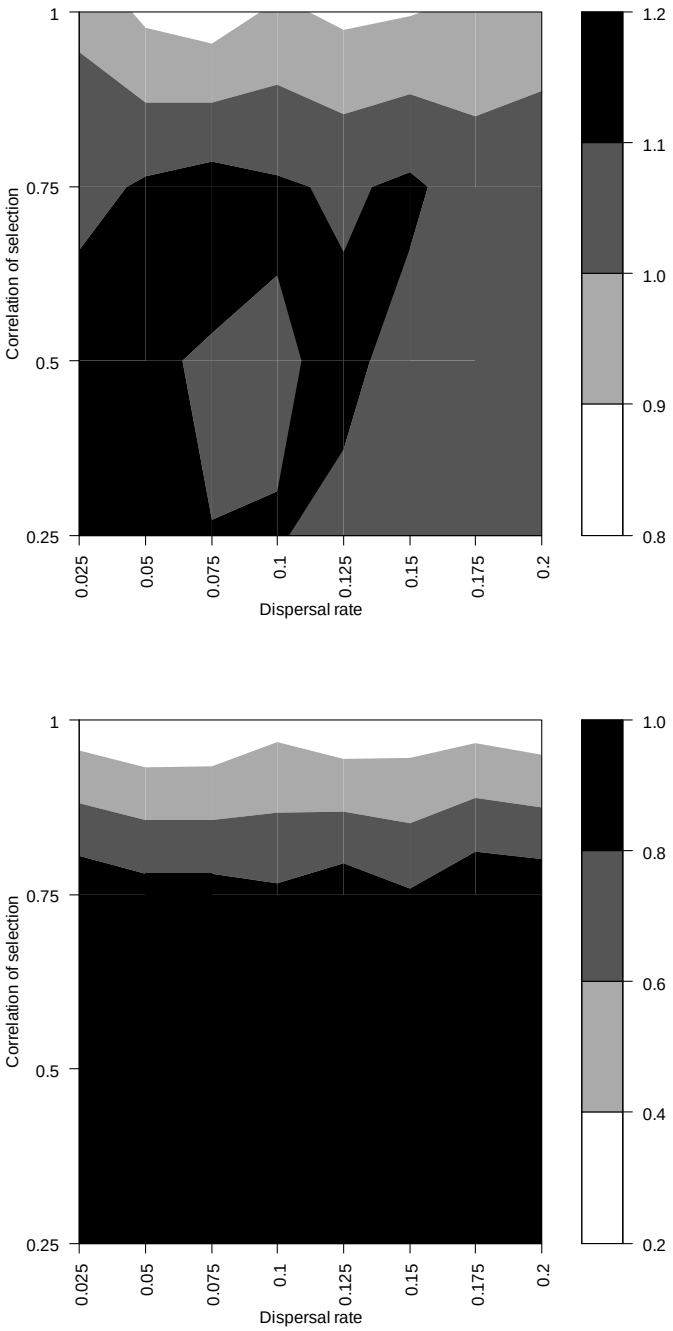


Figure 4.19. Contour plots of mean reproductive success in females (top) and males (bottom) in the stream population. The beach population showed similar patterns and is therefore not shown here. The correlation of selection on body length and depth is unitless and is positively related to the strength of stabilizing selection, and dispersal rate corresponds to the proportion of individuals within each population that disperse.



4.20. Contour plots of relative reproductive success (strays to non-dispersers) in females (top) and males (bottom) in the stream population. The beach population showed similar patterns and is therefore not shown here. The correlation of selection on body length and depth is unitless and is positively related to the strength of stabilizing selection, and dispersal rate corresponds to the proportion of individuals within each population that disperse.

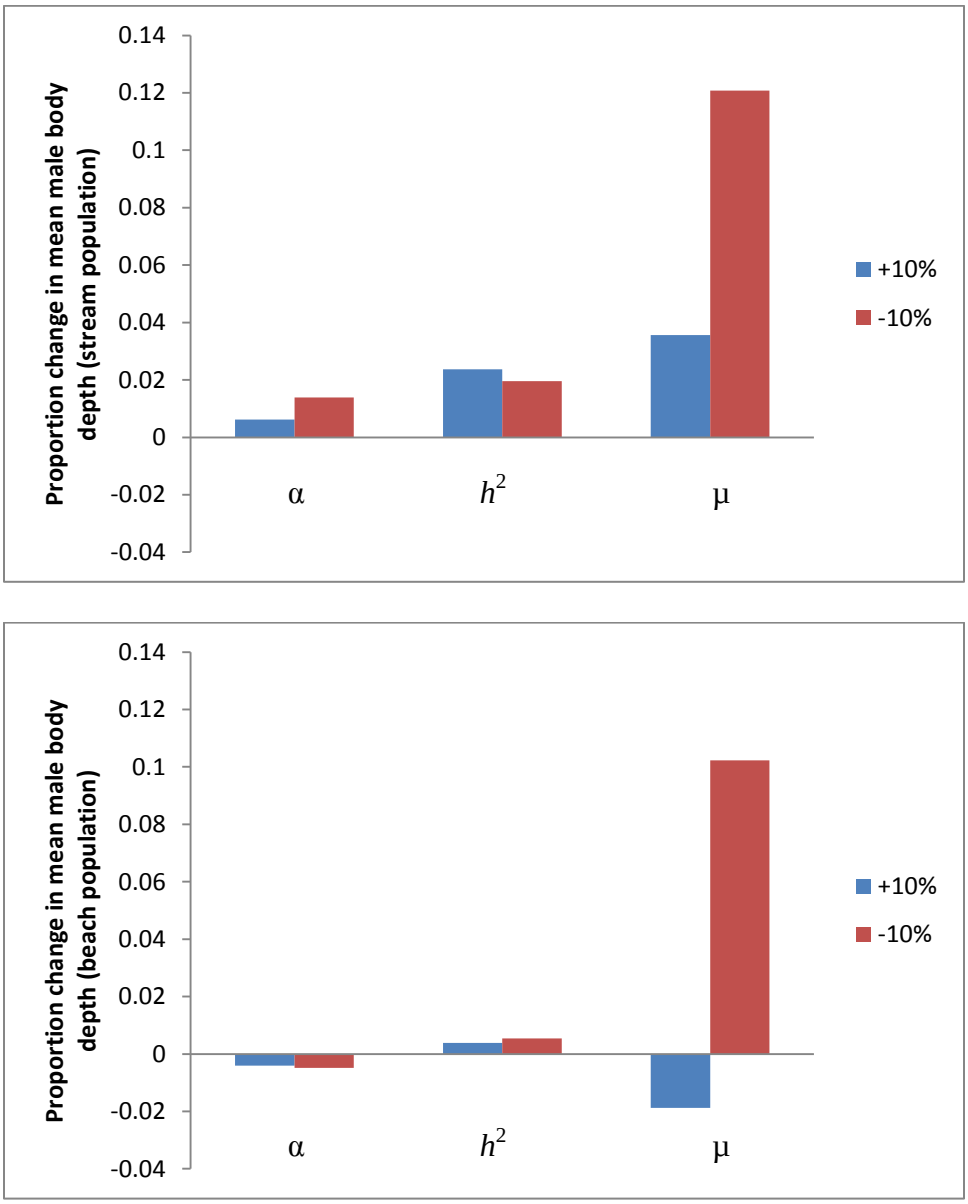


Figure 4.21. Sensitivity of mean male body depth (mm) in the stream population (top) and the beach population (bottom) to changes in the following parameters, ordered from left to right in the figure: Ricker model productivity (α), heritability (h^2) and body length of peak vulnerability to harvest (μ). The parameters were increased by 10% (blue bars) and decreased by 10% (red bars) for the analysis. Plots for body length look very similar and are not shown here.

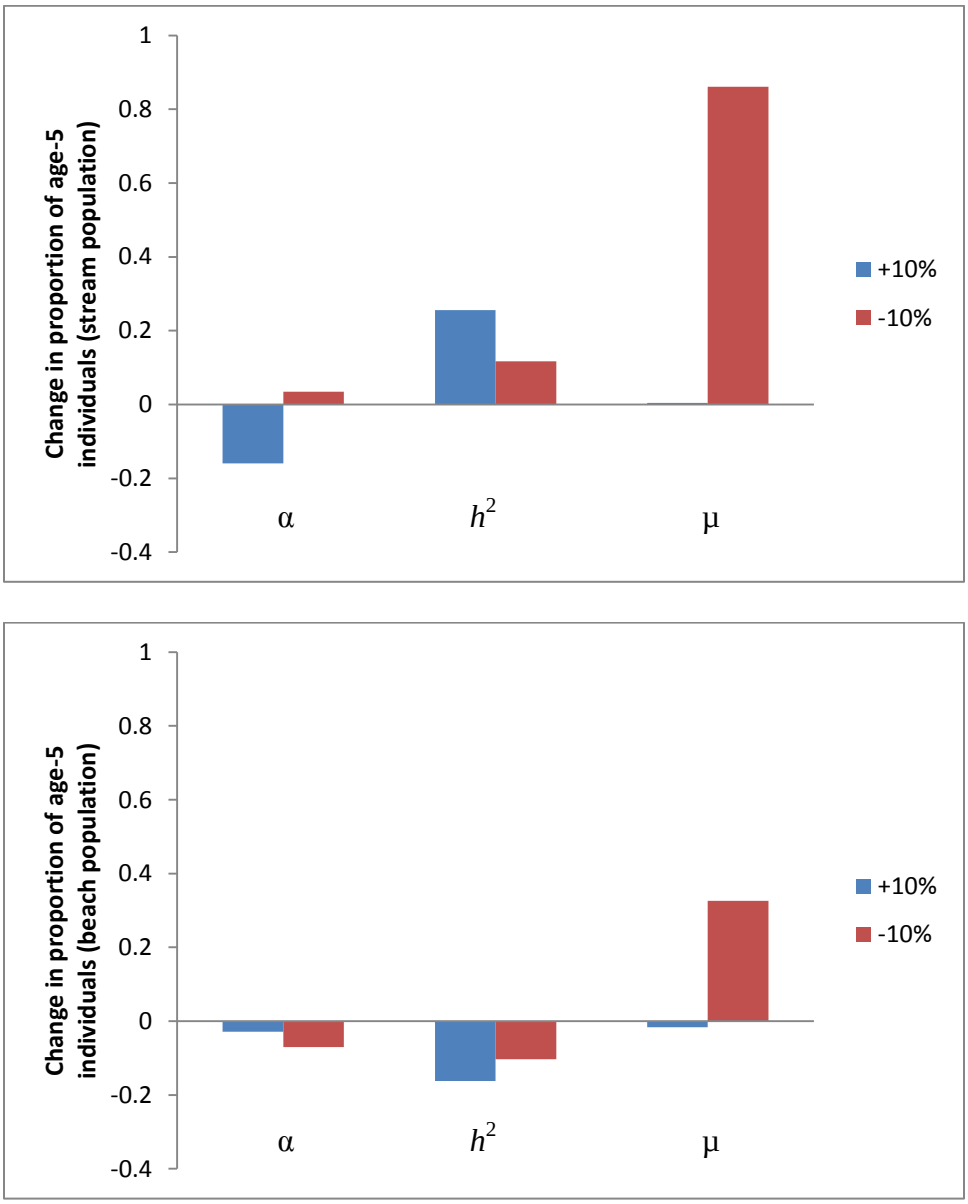


Figure 4.22. Sensitivity of proportion of age-5 individuals in the stream population (top) and the beach population (bottom) to changes in the following parameters, ordered from left to right in the figure: Ricker model productivity (α), heritability (h^2) and body length of peak vulnerability to harvest (μ). The parameters were increased by 10% (blue bars) and decreased by 10% (red bars) for the analysis.

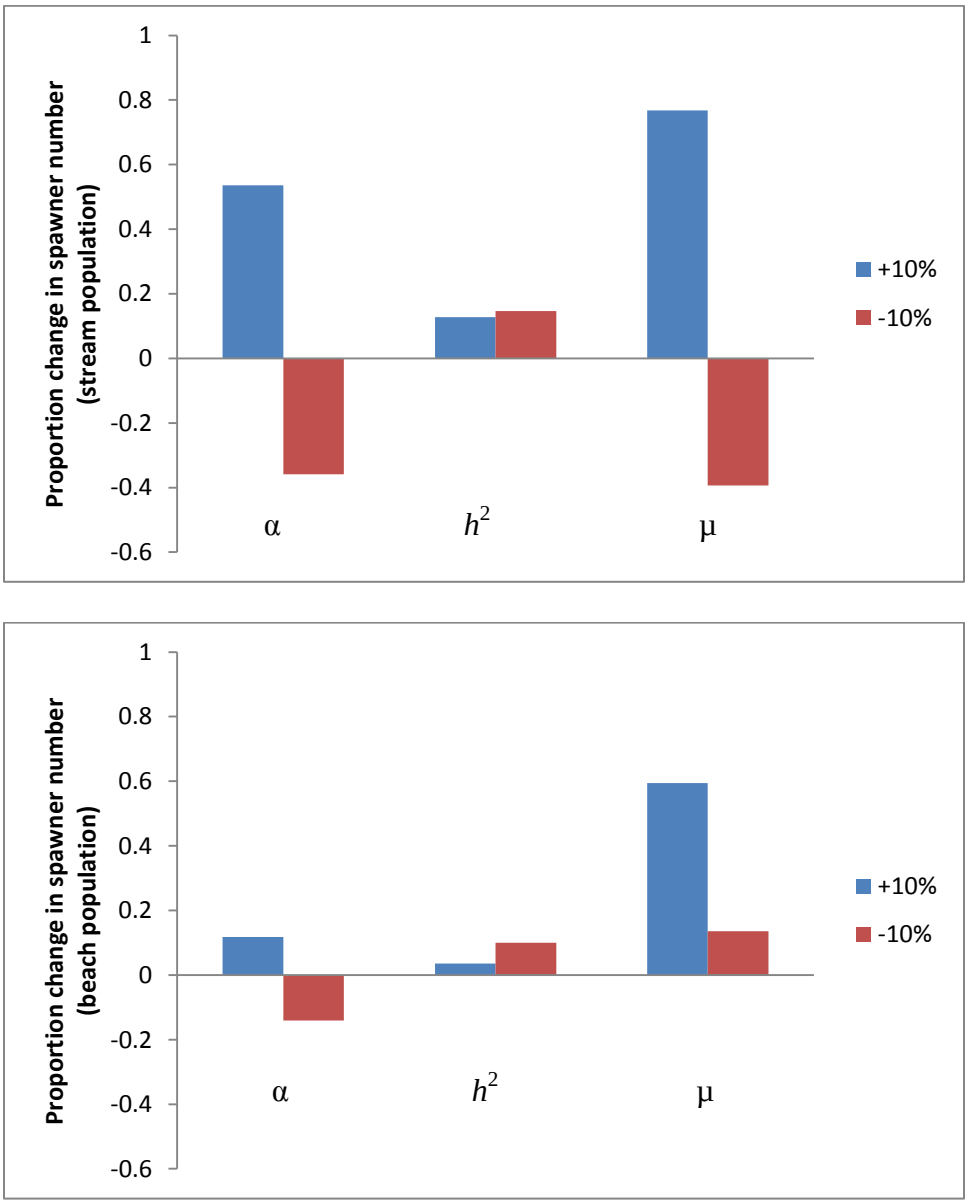


Figure 4.23. Sensitivity of spawner number in the stream population (top) and the beach population (bottom) to changes in the following parameters, ordered from left to right in the figure: Ricker model productivity (α), heritability (h^2) and body length of peak vulnerability to harvest (μ). The parameters were increased by 10% (blue bars) and decreased by 10% (red bars) for the analysis.

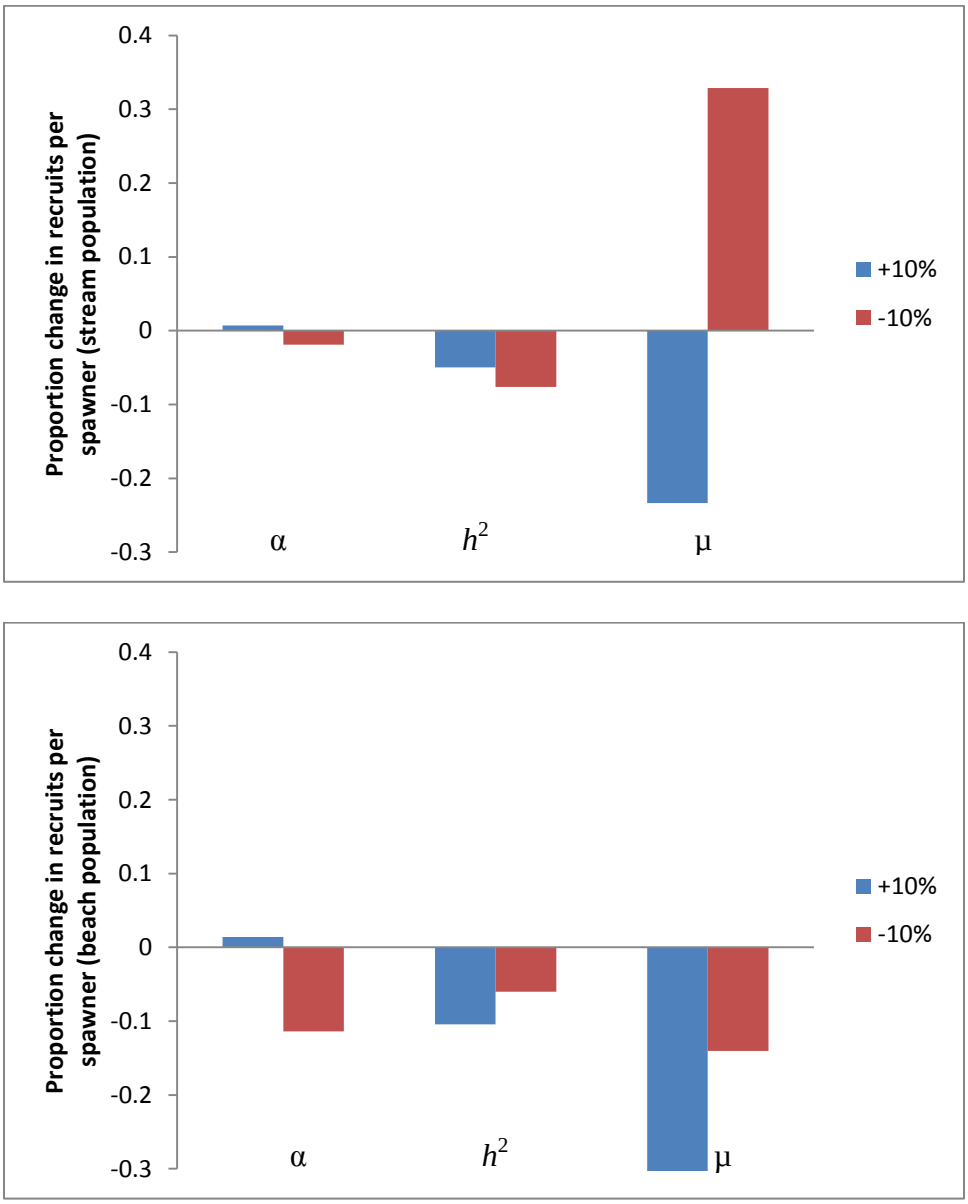


Figure 4.24. Sensitivity of recruits per spawner in the stream population (top) and the beach population (bottom) to changes in the following parameters, ordered from left to right in the figure: Ricker model productivity (α), heritability (h^2) and body length of peak vulnerability to harvest (μ). The parameters were increased by 10% (blue bars) and decreased by 10% (red bars) for the analysis.

Table 4.1. 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 (years)	4.2	4.3	4.3	4.1
Std dev age (years)	0.4	0.5	0.5	0.3
Mean length (mm)	432	444	425	452
Std dev length (mm)	29	23	27	32
Mean depth (mm)	108	131	111	144
Std dev depth (mm)	11	15	17	17

Table 4.2. Phenotypic variance-covariance matrices for each sex and population, calculated from empirical data on A Creek and A Beach sockeye salmon. In each of these matrices, the first trait is age at maturity (years), the second trait is body length at maturity (mm), and the third trait is body depth at maturity (mm).

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

Table 4.3. ***G*** matrices for age-specific body length (mm), age-specific body depth (mm), and age (years) for the stream population (top) and the beach population (bottom).

	Age3 length	Age3 depth	Age4 length	Age4 depth	Age5 length	Age5 depth	Continuous age
Age3 length	86.7	30.6	71.1	36.7	75.0	42.8	2.7
Age3 depth	30.6	30.0	41.8	21.6	44.1	25.2	1.6
Age4 length	71.1	41.8	162.0	50.2	102.5	58.6	3.7
Age4 depth	36.7	21.6	50.2	43.2	52.9	30.2	1.9
Age5 length	75.0	44.1	102.5	52.9	180.0	61.7	3.9
Age5 depth	42.8	25.2	58.6	30.2	61.7	58.8	2.3
Cont. age	2.7	1.6	3.7	1.9	3.9	2.3	0.2

	Age3 length	Age3 depth	Age4 length	Age4 depth	Age5 length	Age5 depth	Continuous age
Age3 length	90.0	31.2	71.7	37.4	88.2	43.7	2.8
Age3 depth	31.2	30.0	41.4	21.6	50.9	25.2	1.6
Age4 length	71.7	41.4	158.7	49.7	117.1	58.0	3.7
Age4 depth	37.4	21.6	49.7	43.2	61.1	30.2	1.9
Age5 length	88.2	50.9	117.1	61.1	240.0	71.3	4.6
Age5 depth	43.7	25.2	58.0	30.2	71.3	58.8	2.3
Cont. age	2.8	1.6	3.7	1.9	4.6	2.3	0.2

Table 4.4. Differences (mm) between traits at age used for back-calculating trait values at all possible ages at maturity for each individual.

	Age 3 to 4	Age 4 to 5	Age 3 to 5
Female length	+80	+20	+100
Female depth	+25	+15	+40
Male length	+120	+30	+150
Male depth	+30	+20	+50

Table 4.5. Parameter values for age (years), body length (mm), and body depth (mm) at maturity.

Parameter	Stream female	Stream male	Beach female	Beach male
Mean age	4.5	4.5	5.2	5.2
Std dev age	0.4	0.6	0.6	0.6
Mean length	430	440	460	490
Std dev length	30	35	35	35
Mean depth	115	140	135	180
Std dev depth	15	20	15	20
Cut-point btwn ages 3 and 4	2	2	2	2
Cut-point btwn ages 4 and 5	4.5	4.5	4.2	4.2

Table 4.6. Mean proportion of strays relative to the total number of successfully spawning individuals in each population, at each dispersal rate. The corrected proportion of strays has been corrected for removal of strays by predation. Variances in the proportion of strays were always very low (< 0.001).

Dispersal rate	Proportion strays, stream (uncorrected)	Proportion strays, stream (corrected)	Proportion strays, beach
0.025	0.036	0.028	0.027
0.050	0.091	0.072	0.055
0.075	0.111	0.087	0.086
0.100	0.148	0.117	0.113
0.125	0.187	0.148	0.142
0.150	0.223	0.176	0.166
0.175	0.263	0.208	0.189
0.200	0.309	0.244	0.216

References

ADF&G (2011) Alaska Freshwater Fish Inventory. Alaska Department of Fish and Game, Division of Sport Fish.

Allendorf F, Waples R (1996) Conservation and genetics of salmonid fishes. In: *Conservation Genetics: Case Histories from Nature* (eds. Avise J, Hamrick J), pp. 238-280. Chapman and Hall, New York.

Anderson J, Faulds P, Atlas W, Pess G, Quinn T (2010) Selection on breeding date and body size in colonizing coho salmon, *Oncorhynchus kisutch*. *Molecular Ecology* **19**, 2562-2573.

Arnold S, Bürger R, Hohenlohe P, Ajie B, Jones A (2008) Understanding the evolution and stability of the G-matrix. *Evolution* **62**, 2451-2461.

Arnold S, Pfrender M, Jones A (2001) The adaptive landscape as a conceptual bridge between micro- and macroevolution. *Genetica* **112**, 9-32.

Arnold S, Wade M (1984) On the measurement of natural and sexual selection: theory. *Evolution* **38**, 709-719.

Ashley MV, Willson MF, Pergams ORW, *et al.* (2003) Evolutionarily enlightened management. *Biological Conservation* **111**, 115-123.

Baker T, Fair L, Clark R, Hasbrouck J (2006) Review of salmon escapement goals in Bristol Bay, Alaska, 2006. Alaska Department of Fish and Game, Fisheries Manuscript 06-05, Anchorage, AK.

Banks MA, Blouin MS, Baldwin BA, *et al.* (1999) Isolation and inheritance of novel microsatellites in Chinook salmon (*Oncorhynchus tschawytscha*). *Journal of Heredity* **90**, 281-288.

Beacham TD, Margolis L, Nelson RJ (1998) A comparison of methods for stock identification for sockeye salmon (*Oncorhynchus nerka*) in Barkley Sound, British Columbia. *North Pacific Anadromous Fish Commission Bulletin* **1**, 227-239.

Beaudouin R, Monod G, Ginot V (2008) Selecting parameters for calibration via sensitivity analysis: An indlividual-based model of mosquitofish population dynamics. *Ecological Modelling* **218**, 29-48.

Belkhir K, Castric V, Bonhomme F (2002) IDENTIX, a software to test for relatedness in a population using permutation methods. *Molecular Ecology Notes* **2**, 611-614.

Bell G (2010) Fluctuating selection: the perpetual renewal of adaptation in variable environments. *Philosophical Transactions of the Royal Society B-Biological Sciences* **365**, 87-97.

Blair GR, Rogers DE, Quinn TP (1993) Variation in life history characteristics and morphology of sockeye salmon in the Kvichak River System, Bristol Bay, Alaska. *Transactions of the American Fisheries Society* **122**, 550-559.

Bradford M, Irvine J (2000) Land use, fishing, climate change, and the decline of Thompson River, British Columbia, coho salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 13-16.

Bridle J, Vines T (2007) Limits to evolution at range margins: when and why does adaptation fail? *Trends in Ecology & Evolution* **22**, 140-147.
Brodie E, Moore A, Janzen F (1995) Visualizing and quantifying natural selection. *Trends in Ecology & Evolution* **10**, 313-318.
Bromaghin J, Nielson R, Hard J (2011) A model of Chinook salmon population dynamics incorporating size-selective exploitation and inheritance of polygenic correlated traits. *Natural Resource Modeling* **24**, 1-47.
Buchholz WG, Miller SJ, Spearman WJ (2001) Isolation and characterization of chum salmon microsatellite loci and use across species. *Animal Genetics* **32**, 162-165.
Burnham K, Anderson D (2002) *Model Selection and Multimodel Inference: a Practical Information-Theoric Approach*, 2nd edn. Springer-Verlag, New York, NY.
Cairney M, Taggart JB, Hoyheim B (2000) Characterization of microsatellite and minisatellite loci in Atlantic salmon (*Salmo salar* L.) and cross-species amplification in other salmonids. *Molecular Ecology* **9**, 2175-2178.
Carlson S, Hilborn R, Hendry A, Quinn T (2007) Predation by bears drives senescence in natural populations of salmon. *Plos One* **2**, e1286.
Carlson S, Rich H, Quinn T (2009) Does variation in selection imposed by bears drive divergence among populations in the size and shape of sockeye salmon? *Evolution* **63**, 1244-1261.
Carlson SM, Quinn TP (2007) Ten years of varying lake level and selection on size-at-maturity in Sockeye Salmon. *Ecology* **88**, 2620-2629.
Carlson SM, Seamons TR (2008) A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. *Evolutionary Applications* **1**, 222-238.
Clark W (1959) Kodiak bear-red salmon relationships at Karluk Lake, Alaska. *Twenty-fourth North American Wildlife Conference* **24**, 337-345.
Conover D, Munch S (2002) Sustaining fisheries yields over evolutionary time scales. *Science* **297**, 94-96.
Cooper A, Mangel M (1999) The dangers of ignoring metapopulation structure for the conservation of salmonids. *Fishery Bulletin* **97**, 213-226.
Cornuet J, Piry S, Luikart G, Estoup A, Solignac M (1999) New methods employing multilocus genotypes to select or exclude populations as origins of individuals. *Genetics* **153**, 1989-2000.
Coulson T, Benton T, Lundberg P, *et al.* (2006) Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proceedings of the Royal Society B-Biological Sciences* **273**, 547-555.
Coulson T, Rohani P, Pascual M (2004) Skeletons, noise and population growth: the end of an old debate? *Trends in Ecology & Evolution* **19**, 359-364.
Coulson T, Tuljapurkar S, Childs D (2010) Using evolutionary demography to link life history theory, quantitative genetics and population ecology. *Journal of Animal Ecology* **79**, 1226-1240.
Cramer J (2003) The origins and development of the logit model. University of Amsterdam and Tinbergen Institute, Amsterdam.

Demory RL, Orrel RF, Heinle DF (1964) Spawning ground catalog of the Kvichak River system, Bristol Bay, Alaska. United States Fish and Wildlife Service Special Scientific Report.

Dias P (1996) Sources and sinks in population biology. *Trends in Ecology & Evolution* **11**, 326-330.

Dickerson B, Brinck K, Willson M, Bentzen P, Quinn T (2005) Relative importance of salmon body size and arrival time at breeding grounds to reproductive success. *Ecology* **86**, 347-352.

Dieckmann U, Heino M (2007) Probabilistic maturation reaction norms: their history, strengths, and limitations. *Marine Ecology-Progress Series* **335**, 253-269.

Doctor K, Hilborn R, Rowse M, Quinn T (2010) Spatial and temporal patterns of upriver migration by sockeye salmon populations in the Wood River System, Bristol Bay, Alaska. *Transactions of the American Fisheries Society* **139**, 80-91.

El Mousadik A, Petit R (1996) High level of genetic differentiation for allelic richness among populations of the argan tree [Argania spinosa (L) Skeels] endemic to Morocco. *Theoretical and Applied Genetics* **92**, 832-839.

Eldridge W, Hard J, Naish K (2010) Simulating fishery-induced evolution in chinook salmon: the role of gear, location, and genetic correlation among traits. *Ecological Applications* **20**, 1936-1948.

Ellner S, Rees M (2006) Integral projection models for species with complex demography. *American Naturalist* **167**, 410-428.

Endler J (1980) Natural selection on color patterns in *Poecilia reticulata*. *Evolution* **34**, 76-91.

Esin E, Leman V (2008) Distribution of fish and the biotopic structure of the basin of the Small Salmon River (the Nachilova River, Western Kamchatka). *Journal of Ichthyology* **48**, 57-67.

Excoffier L, Lischer H (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources* **10**, 564-567.

Falconer DS, McKay TFC (1996) *Introduction to Quantitative Genetics* Prentice Hall, Harlow, England.

Falush D, Stephens M, Pritchard J (2007) Inference of population structure using multilocus genotype data: dominant markers and null alleles. *Molecular Ecology Notes* **7**, 574-578.

Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics* **164**, 1567-1587.

Faubet P, Gaggiotti O (2008) A new Bayesian method to identify the environmental factors that influence recent migration. *Genetics* **178**, 1491-1504.

Faubet P, Waples R, Gaggiotti O (2007) Evaluating the performance of a multilocus Bayesian method for the estimation of migration rates. *Molecular Ecology* **16**, 1149-1166.

Fillatre EK, Etherton P, Heath DD (2003) Bimodal run distribution in a northern population of sockeye salmon (*Oncorhynchus nerka*): life history and genetic analysis on a temporal scale. *Molecular Ecology* **12**, 1793-1805.
Fleming I (1998) Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 59-76.
Foote C (1988) Male mate choice dependent on male size in salmon. *Behaviour* **106**, 63-80.
Foote C (1989) Female mate preference in Pacific salmon. *Animal Behaviour* **38**, 721-723.
Ford M, Hard J, Boelts B, Lahood E, Miller J (2008) Estimates of natural selection in a salmon population in captive and natural environments. *Conservation Biology* **22**, 783-794.
Frankham R (1995) Effective population size/adult population size ratios in wildlife: A review. *Genetical Research* **66**, 95-107.
Garant D, Forde SE, Hendry AP (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology* **21**, 434-443.
Garant D, Kruuk L (2005) How to use molecular marker data to measure evolutionary parameters in wild populations. *Molecular Ecology* **14**, 1843-1859.
Garant D, Kruuk L, Wilkin T, McCleery R, Sheldon B (2005) Evolution driven by differential dispersal within a wild bird population. *Nature* **433**, 60-65.
Gard R (1971) Brown bear predation on sockeye salmon at Karluk Lake, Alaska. *Journal of Wildlife Management* **35**, 193-204.
Ghalambor CK, McKay JK, Carroll SP, Reznick DN (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology* **21**, 394-407.
Gharrett AJ, Shirley SM, Tromble GR (1987) Genetic relationships among populations of Alaskan chinook Salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 765-774.
Gilk S, Wang I, Hoover C, *et al.* (2004) Outbreeding depression in hybrids between spatially separated pink salmon, *Oncorhynchus gorbuscha*, populations: marine survival, homing ability, and variability in family size. *Environmental Biology of Fishes* **69**, 287-297.
Gomez-Uchida D, Seeb J, Smith M, *et al.* (2011) Single nucleotide polymorphisms unravel hierarchical divergence and signatures of selection among Alaskan sockeye salmon (*Oncorhynchus nerka*) populations. *Bmc Evolutionary Biology* **11**, 48.
Goudet J (1995) FSTAT v1.2. A computer program to calculate F-statistics. *Journal of Heredity* **86**, 485-486.
Graham M (2003) Confronting multicollinearity in ecological multiple regression. *Ecology* **84**, 2809-2815.
Greig C, Banks MA (1999) Five multiplexed microsatellite loci for rapid response run identification of California's endangered winter Chinook salmon. *Animal Genetics* **30**, 318-320.

Greig C, Jacobson DP, Banks MA (2003) New tetranucleotide microsatellites for fine-scale discrimination among endangered Chinook salmon (*Oncorhynchus tshawytscha*). *Molecular Ecology Notes* **3**, 376-379.
Grimm V (1999) Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling* **115**, 129-148.
Grimm V, Berger U, Bastiansen F, *et al.* (2006) A standard protocol for describing individual-based and agent-based models. *Ecological Modelling* **198**, 115-126.
Groot C, Margolis L (1991) *Pacific Salmon Life Histories* University of British Columbia Press, Vancouver, Canada.
Guillaume F, Rougemont J (2006) Nemo: an evolutionary and population genetics programming framework. *Bioinformatics* **22**, 2556-2557.
Guillaume F, Whitlock M (2007) Effects of migration on the genetic covariance matrix. *Evolution* **61**, 2398-2409.
Guo SW, Thompson EA (1992) Performing the exact test of Hardy-Weinberg proportion for multiple alleles. *Biometrics* **48**, 361-372.
Hadfield J (2010) MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software* **33**, 1-22.
Hard J, Gross M, Heino M, *et al.* (2008) Evolutionary consequences of fishing and their implications for salmon. *Evolutionary Applications* **1**, 388-408.
Hard JJ (1995) A quantitative genetic perspective on the conservation of intraspecific diversity. *American Fisheries Society Symposium* **17**, 304-326.
Harshman L, Hoffmann A (2000) Laboratory selection experiments using *Drosophila*: what do they really tell us? *Trends in Ecology & Evolution* **15**, 32-36.
Hauser L, Baird M, Hilborn R, Seeb L, Seeb J (2011) An empirical comparison of SNPs and microsatellites for parentage and kinship assignment in a wild sockeye salmon (*Oncorhynchus nerka*) population. *Molecular Ecology Resources* **11**, 150-161.
Hendry A, Morbey Y, Berg O, Wenburg J (2004a) Adaptive variation in senescence: reproductive lifespan in a wild salmon population. *Proceedings of the Royal Society of London Series B-Biological Sciences* **271**, 259-266.
Hendry A, Nosil P, Rieseberg L (2007) The speed of ecological speciation. *Functional Ecology* **3**, 455-464.
Hendry AP (2004) Selection against migrants contributes to the rapid evolution of ecologically dependent reproductive isolation. *Evolutionary Ecology Research* **6**, 1219-1236.
Hendry AP, Castric V, Kinnison MT, Quinn TP (2004b) The evolution of philopatry and dispersal: homing versus straying in salmonids. In: *Evolution Illuminated: Salmon and Their Relatives* (eds. Hendry AP, Stearns SC), pp. 52-91. Oxford University Press, Oxford.
Hilborn R, Mangel M (1997) *The Ecological Detective* Princeton University Press, Princeton.

Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003) Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 6564-6568.
Hood G (2002) PopTools. CSIRO, Canberra.
Howard R (1979) Estimating reproductive success in natural populations. *American Naturalist* **114**, 221-231.
Hubisz M, Falush D, Stephens M, Pritchard J (2009) Inferring weak population structure with the assistance of sample group information. *Molecular Ecology Resources* **9**, 1322-1332.
Hurvich C, Tsai CL (1993) A corrected Akaike information criterion for vector autoregressive model selection. *Journal of Time Series Analysis* **14**, 271-279.
Huston M, Deangelis D, Post W (1988) New computer models unify ecological theory. *Bioscience* **38**, 682-691.
Hutchings J, Fraser D (2008) The nature of fisheries- and farming-induced evolution. *Molecular Ecology* **17**, 294-313.
Ihssen PE, Evans, D.O., Christie, W.J., Reckahn, J.A., and DesJardine, R.L. (1981) Life history, morphology, and electrophoretic characteristics of five allopatric stocks of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes region. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1790-1807.
Jaquiery J, Broquet T, Hirzel A, Yearsley J, Perrin N (2011) Inferring landscape effects on dispersal from genetic distances: how far can we go? *Molecular Ecology* **20**, 692-705.
Johnson J, Blanche P (2010) Catalog of waters important for spawning, rearing, or migration of anadromous fishes – Southwestern Region. Alaska Department of Fish and Game, Anchorage, AK.
Johnson P, Haydon D (2007) Software for quantifying and simulating microsatellite genotyping error. *Bioinformatics and Biology Insights* **1**, 71-75.
Jones A, Arnold S, Bürger R (2003) Stability of the G-matrix in a population experiencing pleiotropic mutation, stabilizing selection, and genetic drift. *Evolution* **57**, 1747-1760.
Jones E, Quinn T, Van Alen B (1998) Observer accuracy and precision in aerial and foot survey counts of pink salmon in a southeast Alaska stream. *North American Journal of Fisheries Management* **18**, 832-846.
Jones O, Wang J (2010) COLONY: a program for parentage and sibship inference from multilocus genotype data. *Molecular Ecology Resources* **10**, 551-555.
Kalinowski S, Taper M, Marshall T (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* **16**, 1099-1106.
Kalinowski S, Wagner A, Taper M (2006) ML-RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. *Molecular Ecology Notes* **6**, 576-579.
Kawecki T (2008) Adaptation to marginal habitats. *Annual Review of Ecology Evolution and Systematics* **39**, 321-342.

Kawecki T, Ebert D (2004) Conceptual issues in local adaptation. *Ecology Letters* **7**, 1225-1241.
Kendall N, Hard J, Quinn T (2009) Quantifying six decades of fishery selection for size and age at maturity in sockeye salmon. *Evolutionary Applications* **2**, 523-536.
Kendall N, Quinn T (2009) Effects of population-specific variation in age and length on fishery selection and exploitation rates of sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* **66**, 896-908.
Kendall N, Quinn T (2011) Length and age trends of Chinook salmon in the Nushagak River, Alaska related to commercial and recreational fishery selection and exploitation. *Transactions of the American Fisheries Society* **140**, 611-622.
Kingsolver JG, Hoekstra HE, Hoekstra JM, *et al.* (2001) The strength of phenotypic selection in natural populations. *American Naturalist* **157**, 245-261.
Kinnison M, Hendry A, Stockwell C (2007) Contemporary evolution meets conservation biology II: Impediments to integration and application. *Ecological Research* **22**, 947-954.
Klinka D, Reimchen T (2002) Nocturnal and diurnal foraging behaviour of brown bears (*Ursus arctos*) on a salmon stream in coastal British Columbia. *Canadian Journal of Zoology* **80**, 1317-1322.
Koskinen M, Haugen T, Primmer C (2002) Contemporary fisherian life-history evolution in small salmonid populations. *Nature* **419**, 826-830.
Kruuk LEB, Hill WG (2008) Introduction. Evolutionary dynamics of wild populations: the use of long-term pedigree data. *Proceedings of the Royal Society B-Biological Sciences* **275**, 593-596.
Kuparinen A, Merila J (2007) Detecting and managing fisheries-induced evolution. *Trends in Ecology & Evolution* **22**, 652-659.
Lande R (1979) Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution* **33**, 402-416.
Lande R (1980) Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34**, 292-305.
Lande R, Arnold S (1983) The measurement of selection on correlated characters. *Evolution* **37**, 1210-1226.
Law R (1991) On the quantitative genetics of correlated characters under directional selection in age-structured populations. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **331**, 213-223.
Leberg P (2002) Estimating allelic richness: Effects of sample size and bottlenecks. *Molecular Ecology* **11**, 2445-2449.
Lenormand T (2002) Gene flow and the limits to natural selection. *Trends in Ecology & Evolution* **17**, 183-189.
Lin J, Quinn TP, Hilborn R, Hauser L (2008a) Fine-scale differentiation between sockeye salmon ecotypes and the effect of phenotype on straying. *Heredity* **101**, 341-350.
Lin J, Ziegler E, Quinn TP, Hauser L (2008b) Contrasting patterns of morphological and neutral genetic divergence among geographically proximate populations of sockeye salmon (*Oncorhynchus nerka*) in Lake Aleknagik, Alaska. *Journal of Fish Biology* **73**, 1993-2004.

Lowe W, Allendorf F (2010) What can genetics tell us about population connectivity? *Molecular Ecology* **19**, 3038-3051.
Lynch M, Walsh B (1998) *Genetics and Analysis of Quantitative Traits* Sinauer Assoc., Inc.
Madsen T, Shine R (1993) Temporal variability in sexual selection acting on reproductive tactics and body size in male snakes. *American Naturalist* **141**, 167-171.
Magnhagen C (1991) Predation risk as a cost of reproduction. *Trends in Ecology & Evolution* **6**, 183-185.
Manley W, Kaufman D, Briner J (2001) Pleistocene glacial history of the southern Ahklun Mountains, southwestern Alaska: Soil-development, morphometric, and radiocarbon constraints. *Quaternary Science Reviews* **20**, 353-370.
Manzer J, Miki I (1986) Fecundity and egg retention of some sockeye salmon (*Oncorhynchus nerka*) stocks in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 1643-1655.
Marriott R (1964) Stream catalog of the Wood River system Bristol Bay, Alaska. *US Fish and Wildlife Service Special Scientific Report*, Fisheries No. 494.
Mayama H, Ishida Y (2003) Japanese studies on the early ocean life of juvenile salmon. *North Pacific Anadromous Fish Commission Bulletin* **3**, 41-67.
Mayr E (1963) *Animal species and evolution* Harvard University Press, Cambridge, MA.
McClelland E, Naish K (2007) What is the fitness outcome of crossing unrelated fish populations? A meta-analysis and an evaluation of future research directions. *Conservation Genetics* **8**, 397-416.
McClure M, Holmes E, Sanderson B, Jordan C (2003) A large-scale, multispecies status, assessment: Anadromous salmonids in the Columbia River Basin. *Ecological Applications* **13**, 964-989.
McPhee MV, Quinn TP (1998) Factors affecting the duration of nest defense and reproductive lifespan of female sockeye salmon, *Oncorhynchus nerka*. *Environmental Biology of Fishes* **51**, 369-375.
Metcalf M, Reid J, Cohen M (2004) *Fortran 95/2003 Explained* Oxford University Press, New York, NY.
Moore J, Schindler D (2008) Biotic disturbance and benthic community dynamics in salmon-bearing streams. *Journal of Animal Ecology* **77**, 275-284.
Moore JS, Gow JL, Taylor EB, Hendry AP (2007) Quantifying the constraining influence of gene flow on adaptive divergence in the lake-stream threespine stickleback system. *Evolution* **61**, 2015-2026.
Morstad S, Jones M, Sands T, *et al.* (2010) 2009 Bristol Bay Area Annual Management Report. Alaska Department of Fish and Game, Anchorage, AK.
Murray C, Rosenau M (1989) Rearing of juvenile Chinook salmon in nonnatal tributaries of the lower Fraser River, British Columbia. *Transactions of the American Fisheries Society* **118**, 284-289.
Naish KA, Hard JJ (2008) Bridging the gap between the genotype and the phenotype: linking genetic variation, selection and adaptation in fishes. *Fish and Fisheries* **9**, 396-422.

Nei M (1973) Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences of the United States of America* **70**, 3321-3323.
Neilson J (1992) Sources of error in otolith microstructure examination In: *Otolith microstructure examination and analysis* (eds. Stevenson K, Campana S), pp. 115-126.
Nelson RJ, Beacham TD (1999) Isolation and cross species amplification of microsatellite loci useful for study of Pacific salmon. *Animal Genetics* **30**, 228-229.
Nosil P, Crespi B (2006) Experimental evidence that predation promotes divergence in adaptive radiation. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 9090-9095.
Olesiuk P (1993) Annual prey consumption by harbor seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. *Fishery Bulletin* **91**, 491-515.
Olsen JB, Bentzen P, Seeb JS (1998) Characterization of seven microsatellite loci derived from pink salmon. *Molecular Ecology* **7**, 1087-1089.
Olsen JB, Habicht C, Reynolds J, Seeb JE (2004) Moderately and highly polymorphic microsatellites provide discordant estimates of population divergence in sockeye salmon, Oncorhynchus nerka. *Environmental Biology of Fishes* **69**, 261-273.
Olsen JB, Wilson SL, Kretschmer EJ, Jones KC, Seeb JE (2000) Characterization of 14 tetranucleotide microsatellite loci derived from sockeye salmon. *Molecular Ecology* **9**, 2185-2187.
Palstra F, O'Connell M, Ruzzante D (2007) Population structure and gene flow reversals in Atlantic salmon (*Salmo salar*) over contemporary and long-term temporal scales: effects of population size and life history. *Molecular Ecology* **16**, 4504-4522.
Pascual M, Quinn T (1994) Geographical patterns of straying of fall Chinook salmon (*Oncorhynchus tshawytscha*) from Columbia River (U.S.A) hatcheries. *Aquaculture and Fisheries Management* **25 (Suppl. 2)**, 17-30.
Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* **6**, 288-295.
Pelletier F, Clutton-Brock T, Pemberton J, Tuljapurkar S, Coulson T (2007) The evolutionary demography of ecological change: Linking trait variation and population growth. *Science* **315**, 1571-1574.
Pemberton JM (2008) Wild pedigrees: the way forward. *Proceedings of the Royal Society B: Biological Sciences* **275**, 613-621.
Pess G (2009) *Patterns and Processes of Salmon Colonization*. PhD dissertation, University of Washington.
Piry S, Alapetite A, Cornuet JM, *et al.* (2004) GENECLASS2: A software for genetic assignment and first-generation migrant detection. *Journal of Heredity* **95**, 536-539.
Policansky D, Magnuson JJ (1998) Genetics, metapopulations, and ecosystem management of fisheries. *Ecological Applications* **8**, S119-S123.
Postma E, van Noordwijk A (2005) Gene flow maintains a large genetic difference in clutch size at a small spatial scale. *Nature* **433**, 65-68.

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics* **155**, 945-959.
Pulliam H (1988) Sources, sinks, and population regulation. *American Naturalist* **132**, 652-661.
Pyper B, Peterman R (1999) Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*), 1967-1997. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1716-1720.
Quinn TP (1984) Homing and straying in Pacific salmon. In: *Mechanisms of migration in fishes* (eds. McCleave J, Arnold G, Dodson J, Neill W), pp. 357-362. Plenum Press, New York, NY.
Quinn TP, Kinnison M (1999) Size-selective and sex-selective predation by brown bears on sockeye salmon. *Oecologia* **121**, 273-282.
Quinn TP, Unwin M, Kinnison M (2011) Contemporary divergence in migratory timing of naturalized populations of chinook salmon, *Oncorhynchus tshawytscha*, in New Zealand. *Evolutionary Ecology Research* **13**, 45-54.
Quinn TP (1993) A review of homing and straying of wild and hatchery-produced salmon. *Fisheries Research* **18**, 29-44.
Quinn TP (1999) Revisiting the stock concept in Pacific salmon: insights from Alaska and New Zealand. *Northwest Science* **73**, 312-324.
Quinn TP (2005) *The Behavior and Ecology of Pacific Salmon and Trout* American Fisheries Society, Bethesda.
Quinn TP, Buck GB (2001) Size- and sex-selective mortality of adult sockeye salmon: Bears, gulls, and fish out of water. *Transactions of the American Fisheries Society* **130**, 995-1005.
Quinn TP, Carlson SM, Gende SM, Rich HB (2009) Transportation of Pacific salmon carcasses from streams to riparian forests by bears. *Canadian Journal of Zoology* **87**, 195-203.
Quinn TP, Foote CJ (1994) The effects of body size and sexual dimorphism on the reproductive behavior of sockeye salmon, *Oncorhynchus nerka*. *Animal Behaviour* **48**, 751-761.
Quinn TP, Gende SM, Ruggerone GT, Rogers DE (2003) Density-dependent predation by brown bears (*Ursus arctos*) on sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 553-562.
Quinn TP, Hendry AP, Buck GB (2001a) Balancing natural and sexual selection in sockeye salmon: interactions between body size, reproductive opportunity and vulnerability to predation by bears. *Evolutionary Ecology Research* **3**, 917-937.
Quinn TP, Hendry AP, Wetzel LA (1995) The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (Oncorhynchus nerka). *Oikos* **74**, 425-438.
Quinn TP, Stewart IJ, Boatright CP (2006) Experimental evidence of homing to site of incubation by mature sockeye salmon, *Oncorhynchus nerka*. *Animal Behaviour* **72**, 941-949.

Quinn TP, Unwin MJ, Kinnison MT (2000) Evolution of temporal isolation in the wild: Genetic divergence in timing of migration and breeding by introduced chinook salmon populations. *Evolution* **54**, 1372-1385.

Quinn TP, Wetzel L, Bishop S, Overberg K, Rogers DE (2001b) Influence of breeding habitat on bear predation and age at maturity and sexual dimorphism of sockeye salmon populations. *Canadian Journal of Zoology* **79**, 1782-1793.

Rannala B, Mountain J (1997) Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Sciences of the United States of America* **94**, 9197-9201.

Raymond M, Rousset F (1995) Genepop (Version-1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity* **86**, 248-249.

Reimchen T (2000) Some ecological and evolutionary aspects of bear-salmon interactions in coastal British Columbia. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **78**, 448-457.

Rensel J, Haigh N, Tynan T (2010) Fraser river sockeye salmon marine survival decline and harmful blooms of *Heterosigrna akashiwo*. *Harmful Algae* **10**, 98-115.

Rexroad CE, Coleman RL, Martin AM, Hershberger WK, Killefer J (2001) Thirty-five polymorphic microsatellite markers for rainbow trout (*Oncorhynchus mykiss*). *Animal Genetics* **32**, 317-319.

Reznick D, Endler J (1982) The impact of predation on life-history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* **36**, 160-177.

Reznick D, Rodd F, Cardenas M (1996) Life-history evolution in guppies (Poecilia reticulata: Poeciliidae) .4. Parallelism in life-history phenotypes. *American Naturalist* **147**, 319-338.

Ricker W (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada* **11**, 559-623.

Ricker W (1975) Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* **191**.

Roff D (2010) *Modeling Evolution: an introduction to numerical methods* Oxford University Press, Oxford.

Rogers D (1973) Abundance and size of juvenile sockeye salmon, *Oncorhynchus nerka*, and associated species in Lake Aleknagik, Alaska, in relation to their environment. *Fishery Bulletin* **71**, 1061-1075.

Rogers LA, Schindler DE (2008) Asynchrony in population dynamics of sockeye salmon in southwest Alaska. *Oikos* **117**, 1578-1586.

Ronce O, Kirkpatrick M (2001) When sources become sinks: Migrational meltdown in heterogeneous habitats. *Evolution* **55**, 1520-1531.

Ruggerone G, Hanson R, Rogers D (2000) Selective predation by brown bears (*Ursus arctos*) foraging on spawning sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **78**, 974-981.

Saccheri I, Hanski I (2006) Natural selection and population dynamics. *Trends in Ecology & Evolution* **21**, 341-347.

Salo E (1991) Life history of chum salmon (*Oncorhynchus keta*). In: *Pacific salmon life histories* (eds. Groot C, Margolis L), pp. 231-309. University of British Columbia Press, Canada.
Scarnecchia D, Roper B (2000) Large-scale, differential summer habitat use of three anadromous salmonids in a large river basin in Oregon, USA. *Fisheries Management and Ecology* **7**, 197-209.
Schindler D, Hilborn R, Chasco B, *et al.* (2010) Population diversity and the portfolio effect in an exploited species. *Nature* **465**, 609-612.
Schluter D (1988) Estimating the form of natural selection on a quantitative trait. *Evolution* **42**, 849-861.
Schluter D (1996) Ecological speciation in postglacial fishes. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **351**, 807-814.
Schtickzelle N, Quinn TP (2007) A metapopulation perspective for salmon and other anadromous fish. *Fish and Fisheries* **8**, 297-314.
Seamons T, Bentzen P, Quinn T (2007) DNA parentage analysis reveals inter-annual variation in selection: results from 19 consecutive brood years in steelhead trout. *Evolutionary Ecology Research* **9**, 409-431.
Selkoe K, Watson J, White C, *et al.* (2010) Taking the chaos out of genetic patchiness: seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. *Molecular Ecology* **19**, 3708-3726.
Sexton J, McIntyre P, Angert A, Rice K (2009) Evolution and ecology of species range limits. *Annual Review of Ecology Evolution and Systematics* **40**, 415-436.
Siepielski A, DiBattista J, Carlson S (2009) It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecology Letters* **12**, 1261-1276.
Simpson G (1944) *Tempo and Mode in Evolution* Columbia University Press, New York, NY.
Slatkin M (1987) Gene flow and the geographic structure of natural populations. *Science* **236**, 787-792.
Smith CT, Koop BF, Nelson RJ (1998) Isolation and characterization of coho salmon (*Oncorhynchus kisutch*) microsatellites and their use in other salmonids. *Molecular Ecology* **7**, 1614-1616.
Steppan SJ, Philips PC, Houle D (2002) Comparative quantitative genetics: evolution of the G matrix. *Trends in Ecology & Evolution* **17**, 320-327.
Stinchcombe J, Agrawal A, Hohenlohe P, Arnold S, Blows M (2008) Estimating nonlinear selection gradients using quadratic regression coefficients: Double or nothing ? *Evolution* **62**, 2435-2440.
Stockwell CA, Hendry AP, Kinnison MT (2003) Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution* **18**, 94-101.
Taylor EB (1991) A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* **98**, 185-207.
Team RDC (2011) R: a language and environment for statistical computing, Vienna, Austria.
Tufto J (2010) Gene flow from domesticated species to wild relatives: migration load in a model of multivariate selection. *Evolution* **64**, 180-192.

Vamosi S (2005) On the role of enemies in divergence and diversification of prey: a review and synthesis. *Canadian Journal of Zoology* **83**, 894-910.
van Oosterhout D, Hutchison WF, Wills DPM, Shipley P (2004) MICROCHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes* **4**, 535-538.
Varnavskaya NV, Wood CC, Everett RJ, *et al.* (1994) Genetic differentiation of subpopulations of sockeye salmon (*Oncorhynchus nerka*) within lakes of Alaska, British-Columbia, and Kamchatka, Russia. *Canadian Journal of Fisheries and Aquatic Sciences* **51 (Suppl. 1)**, 147-157.
Visscher P, Hill W, Wray N (2008) Heritability in the genomics era - concepts and misconceptions. *Nature Reviews Genetics* **9**, 255-266.
Walker J (1997) Ecological morphology of lacustrine threespine stickleback *Gasterosteus aculeatus* L (Gasterosteidae) body shape. *Biological Journal of the Linnean Society* **61**, 3-50.
Walling C, Pemberton J, Hadfield J, Kruuk L (2010) Comparing parentage inference software: reanalysis of a red deer pedigree. *Molecular Ecology* **19**, 1914-1928.
Waples R (1991) Pacific Salmon, *Oncorhynchus* spp. & the definition of 'species' under the endangered species act. *Marine Fisheries Reviews* **53**, 11-22.
Waples RS (1990) Conservation genetics of Pacific salmon. II. Effective population size and the rate of loss of genetic variability. *Journal of Heredity* **81**, 267-276.
Waples RS, Do C (2008) LDNE: A program for estimating effective population size from data on linkage disequilibrium. *Molecular Ecology Resources* **8**.
Watkinson A, Sutherland W (1995) Sources, sinks, and pseudo-sinks. *Journal of Animal Ecology* **64**, 126-130.
Weir BS, Cockerham CC (1984) Estimating F-Statistics for the analysis of population structure. *Evolution* **38**, 1358-1370.
Whitlock MC, McCauley DE (1999) Indirect measures of gene flow and migration: FST not equal to 1/(4Nm+1). *Heredity* **82**, 117-125.
Williamson KS, Cordes JF, May B (2002) Characterization of microsatellite loci in chinook salmon (*Oncorhynchus tshawytscha*) and cross-species amplification in other salmonids. *Molecular Ecology Notes* **2**, 17-19.
Wilmot RL, Everett RJ, Spearman WJ, *et al.* (1994) Genetic stock structure of Western Alaska chum salmon and a comparison with Russian Far-East stocks. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 84-94.
Wilson A, Reale D, Clements M, *et al.* (2010) An ecologist's guide to the animal model. *Journal of Animal Ecology* **79**, 13-26.
Wilson W (1998) Resolving discrepancies between deterministic population models and individual-based simulations. *American Naturalist* **151**, 116-134.
Wood CC (1995) Life history variation and population structure in sockeye salmon. *American Fisheries Society Symposium* **17**, 195-216.
Wright S (1931) Evolution in Mendelian populations. *Genetics* **16**, 97-159.
Zuur A, Ieno E, Walker N, Saveliev A, Smith G (2009) *Mixed effects models and extensions in ecology with R* Springer Science, New York, NY.