

# Ecological factors influencing lifetime productivity of pink salmon (*Oncorhynchus gorbuscha*) in an Alaskan stream

Christopher V. Manhard, John E. Joyce, William W. Smoker, and Anthony J. Gharrett

**Abstract:** Ecological factors underlying freshwater productivity and marine survival of pink salmon (*Oncorhynchus gorbuscha*) were evaluated by analyzing a 30 year time series of local environmental data and censuses of migrating adult and juvenile fish collected at Auke Creek, Alaska. Freshwater productivity was influenced primarily by spawning habitat limitation and less so by stream temperature and flow. Furthermore, a trend of declining freshwater productivity was detected over the time series, which may be related to observed declines in spawning substrate quality and in the duration of the adult migration. Marine survival was highly variable among brood years and was influenced by physical conditions in the nearshore marine environment; warm sea-surface temperatures during nearshore residency were associated with higher marine survival rates, whereas high stream flows late in the fry emigration period were associated with reduced marine survival. Simulations of adult recruitment, based on ecological factors in the freshwater and marine environments, indicated that the productivity of pink salmon in this stream is determined primarily by early marine survival.

**Résumé :** Les facteurs écologiques qui sous-tendent la productivité en eau douce et la survie en mer du saumon rose (*Oncorhynchus gorbuscha*) ont été évalués en analysant une série chronologique de 30 ans de données environnementales locales et des recensements de poissons adultes et juvéniles en migration prélevés du ruisseau Auk (Alaska). La productivité en eau douce était principalement influencée par des limites associées à l'habitat de frai, moins par la température ou le débit du cours d'eau. En outre, une tendance à la baisse de la productivité en eau douce a été décelée sur la série chronologique, qui pourrait être reliée à des diminutions observées de la qualité des substrats de frai et de la durée de la migration des adultes. La survie en mer était très variable entre les années d'éclosion et influencée par des conditions physiques dans le milieu marin littoral; des températures élevées de la surface de la mer durant la résidence en milieu littoral étaient associées à des taux de survie en mer plus élevés, alors que des débits forts tard durant l'émigration des alevins étaient associés à un taux de survie en mer réduit. Des simulations du recrutement d'adultes basées sur des facteurs écologiques dans les milieux d'eau douce et marins indiquent que la productivité du saumon rose dans ce cours d'eau est principalement déterminée par la survie précoce en mer. [Traduit par la Rédaction]

## Introduction

The anadromous life cycle of Pacific salmon (*Oncorhynchus* spp.) entails exposure to a diverse array of ecological factors during their freshwater and marine stages. An understanding of which of these factors drive productivity can provide a basis for addressing fisheries research topics, such as the extent to which habitat availability and seasonal environmental variation control reproduction and survival and whether lifetime productivity is primarily limited by the freshwater or marine stage. Additionally, the identification of links between environmental variation and demographic processes can enhance our understanding of how salmonid populations will respond to climate change. These research topics have important implications for the development of salmonid management strategies.

Studies of ecological components of salmonid productivity have largely focused on either the freshwater or the marine stage. In the freshwater environment, density-dependent factors that arise from limited spawning habitat, such as redd superimposition (Fukushima et al. 1998), can limit fry production (Essington et al. 2000; Gharrett et al. 2013). However, water conditions, temperature, and flow in particular may also be important to fry

production because of their effects on spawning efficiency and embryo survival (Murphy 1985; Gibson and Myers 1988; Montgomery et al. 1996). In the marine environment, there is evidence that overall marine survival is primarily determined by survival of fry during their initial marine residency (Beamish et al. 2004; Moss et al. 2005; Farley et al. 2007). Physical factors, such as sea-surface temperature and freshwater input into the nearshore environment, likely have a large bearing on survival during this stage because they condition the potential for growth of fry (Gargett 1997; Mortensen et al. 2000; Royer et al. 2001). While the extensive literature on salmonid ecology has demonstrated that ecological factors in both the freshwater and marine stages can influence lifetime productivity, few studies have incorporated both stages into a single analysis. Such an analysis would provide a basis for measuring the relative importance of each stage and identifying ecological factors that limit lifetime productivity.

The relatively simple life history of pink salmon (*Oncorhynchus gorbuscha*) makes them an excellent species for modeling ecological factors that may underlie lifetime productivity in many anadromous salmonid populations. Because adults nearly always reach maturity in their second year of life throughout their natu-

Received 26 July 2016. Accepted 30 November 2016.

**C.V. Manhard,\* W.W. Smoker, and A.J. Gharrett.** School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau Center, 17101 Point Lena Loop Road, Juneau, AK 99801, USA.

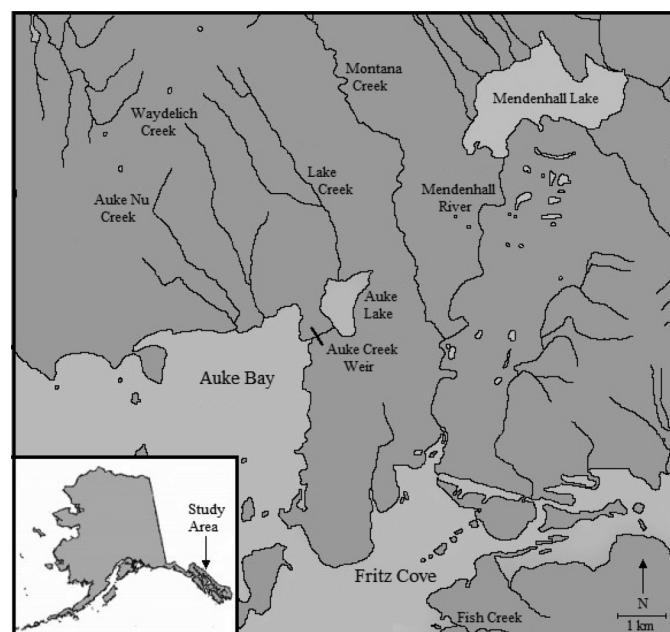
**J.E. Joyce.** National Marine Fisheries Service, Auke Bay Laboratories, Ted Stevens Marine Research Institute, 17109 Point Lena Loop Road, Juneau, AK 99801, USA.

**Corresponding author:** Christopher V. Manhard (email: [cvmanhard@alaska.edu](mailto:cvmanhard@alaska.edu)).

\*Present address: California Cooperative Fish and Wildlife Research Unit, Humboldt State University, 1 Harpst Street, Arcata, CA 95521, USA.

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from [RightsLink](http://RightsLink.com).

**Fig. 1.** Map of Auke Bay, Alaska. The position of the Auke Creek weir is depicted by a bold line. Map data: Google.



ral range (Anas 1959), pink salmon populations have nonoverlapping generations, which obviates the need for age-structure resolution in ecological analyses. Additionally, juvenile pink salmon emigrate to the nearshore marine environment shortly after emerging from the gravel, and this absence of a protracted freshwater period is conducive to identifying ecological factors that underlie reproductive performance.

From time series of census data collected at the permanent salmon weir at Auke Creek Research Station and of environmental data that reflect habitat quality at critical life history periods, we modeled the importance of biotic and abiotic factors to lifetime productivity of pink salmon. These census data included daily counts of both immigrant adults in summer and emigrant juveniles in spring, which conveniently divide the life history into freshwater and marine stages. The primary questions that these analyses address are the following. (1) Are compensatory or depensatory processes evident in the population dynamics of these stages? (2) Which ecological factors drive productivity in these stages? (3) What are the relative contributions of the freshwater and marine stages to lifetime productivity?

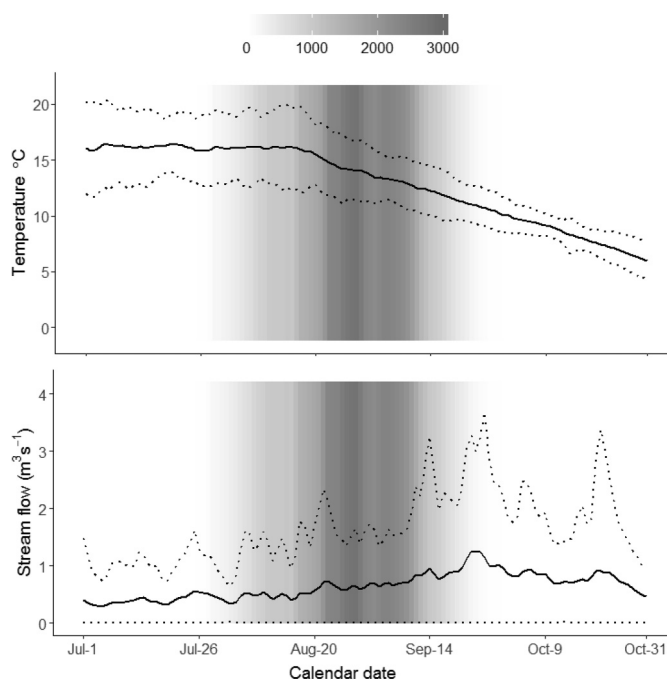
## Materials and methods

### Census data source

#### Study site

Auke Creek, a short (323 m), moderate-gradient (2%–4%) outlet stream that flows from Auke Lake to the estuary of Auke Bay (Fig. 1), is a migratory corridor and spawning ground for pink salmon. In accordance with the strict 2 year life cycle of pink salmon, genetically distinct even- and odd-year brood lines inhabit Auke Creek. Within each brood line, time of return of spawning adults has followed a bimodal distribution; migration into Auke Creek of ‘early’ spawners typically occurs between mid- and late August, whereas migration of ‘late’ spawners typically occurs between early and mid-September (Taylor 1980) (Fig. 2). Although a few of the pink salmon homing to the Auke Lake system spawn in the intertidal area and in Lake Creek, a tributary of Auke Lake, most spawn in the spatially limited (~1000 m<sup>2</sup>) habitat of Auke Creek (Taylor 2008b). Located at the demarcation between intertidal and upstream habitats is Auke Creek Research

**Fig. 2.** Observed stream temperature and estimated stream flow of Auke Creek during late summer and fall. Daily means (solid lines) and 95% prediction intervals (broken lines) are depicted. The historical mean abundance of spawning pink salmon on each day is depicted by a gradation scheme.



Station, a permanent weir and research salmon hatchery that is operated by the US National Marine Fisheries Service. The weir allows for censuses of upstream-spawning adults and emigrating fry.

### Census data

Censuses of emigrating fry have been made at Auke Creek since 1972, but censuses prior to 1980 were made with less accurate fyke nets rather than the permanent counting structure used in later years. In addition to uncertainty about the quality of early juvenile censuses made with nets, there is uncertainty about censuses of wild adults made prior to 1983 because of experimental releases of unmarked fish from the Auke Creek hatchery in the 1970s and early 1980s. Consequently, only censuses of adult salmon made after the fall of 1983 were included in this study. An important consideration in constructing the data sets was the presence of hatchery-reared fish released from the experimental hatchery and of wild fish that were implanted with coded wire tags as part of a straying study (Appendix A, Table A1). For the freshwater productivity models, we excluded all fish of hatchery origin from the data set. For the marine productivity models, we excluded all fish that were hatchery reared or coded wire tagged under the expectation that these processes would negatively bias marine survival. Brood year 1994 was excluded from both data sets because the release of a large number of unmarked experimental fish in 1995 limited our ability to estimate the abundance of wild-origin adults that returned in 1996 (Mortensen et al. 2002). The time series of adult census data included each adult migration period from 1984 to 2013, and the juvenile census data included each fry emigration period from 1983 to 2013. Together, these census data were used to construct separate models of the population dynamics of Auke Creek pink salmon in the freshwater and marine environments over 29 brood years.

### Abundance-based models of productivity

#### Freshwater productivity

We analyzed the relationship between the number of fry that emigrated in spring and the number of adults that returned to

Auke Creek during the previous summer to explore the freshwater population dynamics. Studies of Auke Creek pink salmon have suggested that freshwater productivity may be limited by competition for spawning substrate and by redd superimposition (Fukushima and Smoker 1997; Fukushima et al. 1998; Gharrett et al. 2013). The Ricker model (Ricker 1954) captures such a relationship. It produces a dome-shaped relationship between recruits and spawning stock, which results from the compensatory effect that spawners exert on juvenile production as the spawning stock increases. The form of the Ricker model is given by

$$(1) \quad J_t = S_{t-1} \exp\left(\alpha - \frac{S_{t-1}}{K}\right) \exp(\varepsilon_t)$$

where the number of emigrant fry in the spring of the  $t$ th year ( $J_t$ ) is related to the number of spawners from the previous summer ( $S_{t-1}$ ) by parameters that are intrinsic to the population and describe its productivity ( $\alpha$ ) and carrying capacity ( $K$ ). This model can be rewritten by dividing both sides by the number of spawners and taking the natural logarithm of both sides:

$$(2) \quad \log_e\left(\frac{J_t}{S_{t-1}}\right) = \alpha - \frac{S_{t-1}}{K} + \varepsilon_t$$

$$\varepsilon_t \sim N(0, \sigma^2)$$

The residual errors ( $\varepsilon$ ), which were assumed to be lognormally distributed (Hilborn and Walters 1992), provided an index of interannual variation in freshwater productivity that was likely due to environmental factors.

### Marine productivity

We explored marine-phase population dynamics with models of the relationship between number of adults that returned to Auke Creek in summer and the number of fry that emigrated in the spring of the previous year. In contrast with the freshwater phase, in which a density-dependent relationship between fry and spawners is supported by theory and empirical observations, the population dynamics of the marine phase are less well understood. Because we did not have strong a priori expectations about this relationship, we used a linear model in which the abundances were log transformed to normalize the residuals:

$$(3) \quad \log_e(S_t) = b + \beta \times \log_e(J_{t-1}) + \varepsilon_t$$

$$\varepsilon_t \sim N(0, \sigma^2)$$

where the abundance of spawners in the summer of the  $t$ th year is  $S_t$ , the model intercept is  $b$ , and the abundance of emigrating fry from the spring of the previous year,  $J_{t-1}$ , is related to the abundance of adults by the parameter  $\beta$ . The residual errors ( $\varepsilon$ ) provided an index of interannual variation in marine productivity that likely had an environmental basis.

### Environmentally based models of productivity

We analyzed the residuals from the abundance-based models to estimate effects of environmental factors on freshwater and marine productivity (e.g., Quinn and Niebauer 1995; Mueter et al. 2002). The residuals from each abundance-based model were treated as separate response variables, which were modeled as functions of covariates that were of hypothetical ecological importance to relevant life history stages. Generalized additive models (GAMs) were initially used to explore potential nonlinear relationships between the environmental covariates and residuals. Estimation of GAMs was accomplished with the “mgcv” package in R (R Core Team 2015), which computed the effective degrees of freedom (edf) for each covariate as part of the model-fitting

algorithm. An edf of close to 1 suggested that a nonlinear relationship was unlikely (Wood 2001). Based on the output of each GAM, a nonlinear or linear parametric model was fit for each covariate and subsequently tested for significance with parametric tests ( $F$  tests). Finally, an information theoretic approach based on the Akaike information criterion (AIC) was used to select the suite of covariates and interactions that minimized the information loss and, therefore, comprised the most parsimonious model. The relative probability,  $P_R$ , that the  $i$ th model minimized the information loss was estimated as

$$(4) \quad P_R = \exp\left(\frac{AIC_{\min} - AIC_i}{2}\right)$$

where  $AIC_{\min}$  corresponded to the model with the lowest AIC score (Burnham and Anderson 2002).

### Covariates of freshwater productivity

#### Median adult migration date

We used daily counts of migrating adults to quantify interannual variation in migration date. Because delays in stream entry may lead to density-related constraints on freshwater productivity, such as egg retention and redd superimposition, we computed the median migration date each year as an index of annual timing. We expected it to covary negatively with freshwater productivity because of compensatory effects from increased spawner densities following delayed stream entry.

#### Stream temperature

The potentially deleterious influence of high stream temperatures on early-migrating fish (Fig. 2) was evaluated by estimating an index of the mean stream temperature experienced by the first half of the adult migration. Each early-migrating fish was assumed to have a stream life of 7 days, based on observations of stream life in Auke Creek (Fukushima and Smoker 1997). The mean stream temperature  $\bar{T}_{ij}$  experienced by the  $i$ th fish within the  $j$ th spawning season was estimated by averaging stream temperatures over the period from the date the fish passed the weir to 7 days after that date:

$$(5) \quad \bar{T}_{ij} = \frac{T_t + T_{t+1} + \dots + T_{t+7}}{8}$$

An index of the average stream temperature experienced by early-migrating adults in the  $j$ th spawning season was then estimated by averaging  $\bar{T}_{ij}$  across  $n_j$  returned adults:

$$(6) \quad \bar{T}_j = \frac{\sum_{i=1}^{n_j} \bar{T}_{ij}}{n_j}$$

This index was expected to covary negatively with freshwater productivity because reduced spawning success has been observed in years of high stream temperatures at Auke Creek.

#### Stream flow

Low stream flows are commonly encountered by the first half of the adult migration (Fig. 2) and may be associated with declines in freshwater productivity (Murphy 1985; Fukushima and Smoker 1997). To evaluate this, an index of the average stream flow experienced by early-migrating salmon during each spawning season was estimated with the approach that was detailed for stream temperature. Although measurements of stream flow in Auke Creek were not available during the span of the salmon abundance time series, daily measurements of precipitation at Auke Bay were available from the Auke Bay Laboratories Climatological



Series (ABLCS), an open-access database maintained by the Alaska Fisheries Science Center, and historical measurements of Auke Creek stream flow were available from 1962 to 1975 through the National Water Information System, an open-access database maintained by the US Geological Survey. Following Fukushima (1996), we used those data to model stream flow in late summer and early fall (July–October) as a linear function of precipitation over the previous 16 days (Appendix A, Table A2). The model parameters were then used to estimate stream flow during autumn from 1984 to 2012.

An index of stream flow during the initial incubation period was estimated as the mean flow between 1 September and 31 October each year. The embryo incubation period, which typically begins in late August or September, is marked by heightened flows and frequent freshets (Fig. 2). This index was expected to covary negatively with freshwater productivity because of scouring of embryos in years of high stream flow.

#### Adult migration year

The year of adult migration was included as a covariate to evaluate whether there has been change in freshwater productivity during the time series. Changes in spawning substrate quality (Taylor 2008a) and in the temporal characteristics of the adult migration (Kovach et al. 2012) have occurred over the time series, and these changes may have affected the fry production capacity of Auke Creek.

#### Covariates of marine productivity

##### Juvenile emigration date

We evaluated the effect of interannual variation in fry emigration time on productivity by including the annual median date of the fry migration as a model covariate. Interannual fluctuations in median emigration time may determine whether fry generally encounter sea-surface temperatures and plankton densities that are adequate to support growth upon entering the ocean (Mortensen et al. 2000).

##### Predator abundance

We evaluated whether the timing and magnitude of predator migrations in Auke Bay influence survival of fry by including predator abundance as a model covariate. Two salmonid species that migrate from Auke Creek in spring, coho salmon (*Oncorhynchus kisutch*) smolts and Dolly Varden (*Salvelinus malma*), are counted daily at the weir. These species prey upon fry (Mortensen et al. 2000), and they typically begin migrating into Auke Bay 1–3 weeks after the peak of the fry emigration. Separate indices of predator abundance were estimated as the annual number of each predator counted at the Auke Creek weir prior to the end of the fry migration period, defined as the date on which 95% of fry had emigrated, plus predators counted through 2 weeks after this date, thereby overlapping the initial marine residence period of most fry.

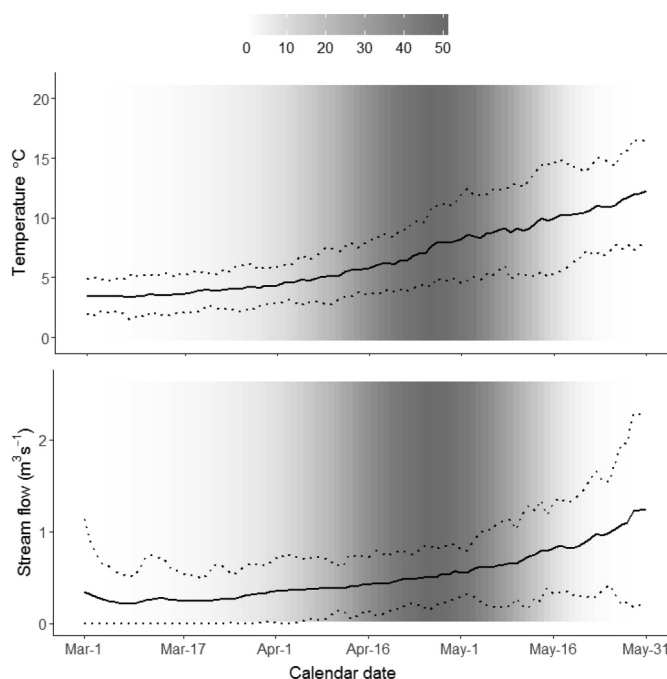
##### Nearshore sea-surface temperature

Because warmer sea-surface temperatures would likely enhance growth and survival of fry, we included sea-surface temperature of Auke Bay as a covariate. Daily sea-surface temperature measurements from the ABLCS (Fig. 3) were averaged from 15 March to 15 May to estimate an index of temperature-related growth opportunity during the fry emigration period.

##### Stream flow

Potential effects of freshwater influx from Auke Creek on marine productivity were evaluated by estimating Auke Creek stream flows during spring (March–May) under the modeling framework described for autumn stream flow (Appendix A, Table A3). The hydrology of the nearshore environment of Auke Bay (Fig. 1) depends on freshwater input from the Auke Lake system as well as its other

**Fig. 3.** Observed sea-surface temperature of Auke Bay and estimated stream flow of Auke Creek during late winter and spring. Daily means (solid lines) and 95% prediction intervals (broken lines) are depicted. The historical mean abundance of pink salmon fry (1000s) in Auke Bay on each day is depicted by a gradation scheme.



major tributaries, which include Waydelich Creek and Auke Nu Creek. Additional freshwater input from the Mendenhall River and Fish Creek, which both discharge into marine waters in nearby Fritz Cove, also influences the nearshore environment of Auke Bay. Since stream flow in these other systems is likely determined by similar environmental factors, Auke Creek was assumed to be a proxy for the aggregate freshwater influx into Auke Bay. An index of freshwater influx in advance of and during the typical extent of the primary plankton bloom (Bienfang and Ziemann 1995) was estimated by averaging stream flow between 1 March and 30 April. This index was expected to covary positively with marine productivity because freshwater input may create mixed layer conditions that support higher food availability. Another index, reflecting the period of high and variable flows that occur late in the nearshore residence period (Fig. 3), was estimated by averaging stream flow between 1 May and 31 May. This index was expected to covary negatively with marine productivity because of offshore displacement of fry or their planktonic prey during years of high stream flows.

##### Emigration year

The year of emigration was included as a covariate to evaluate whether there has been change in marine productivity during the time series. Trends toward warmer vernal sea-surface temperatures have been observed in Auke Bay during the time series (Manhard 2016), which may have affected the quality of habitat encountered by emigrant juveniles.

##### Adult recruitment simulation

The freshwater and marine population dynamics models provided an opportunity to evaluate the relative influence of these life history stages on lifetime productivity. Recruitment of returning adults was used as our metric of lifetime productivity. To estimate adult recruitment, we first estimated the number of fry produced by a given spawner abundance by replacing the residual error term in eq. 2 with the environmentally based model of

freshwater productivity. Next, the estimated fry abundance was substituted into eq. 3. Finally, we replaced the residual error term in eq. 3 with the environmentally based model of marine productivity to estimate adult recruitment. Statistical uncertainty regarding the effect of each covariate on recruitment was quantified by estimating the parameters of the freshwater and marine productivity models under a Bayesian framework. Samples from the posterior distribution of each parameter were drawn with the Markov chain Monte Carlo (MCMC) algorithm, which was performed in R by using the package “rjags” (Plummer 2016) to call JAGS (Plummer 2003) from R. Noninformative and proper priors were used for each  $i$ th parameter:

$$(7) \quad \beta_i \sim N(\mu = 0, \sigma^2 = 1 \times 10^4)$$

Each model was run for 215 000 iterations with a burn-in period of 200 000, and a thinning interval of 5 was used to reduce autocorrelation among posterior samples. Convergence was tested with the Gelman–Rubin convergence diagnostic  $\hat{R}$  (Gelman and Rubin 1992), which compared variance within and between chains.

The relative influence of ecologically relevant covariates on lifetime productivity was evaluated by iteratively simulating recruitment at the values of each covariate during the 30 year time series that minimized ( $R_{\min}$ ) and maximized ( $R_{\max}$ ) recruitment. To isolate the variation attributable to a covariate of interest during its simulation, all other covariates were fixed at their historical means. The simulation was run for 10 000 iterations for each covariate. On each iteration of the simulation, a random draw was made from the posterior distributions of the model parameters and then recruitment was jointly estimated by the freshwater and marine models as previously described. Finally, the difference in recruitment ( $R_{\Delta}$ ) between  $R_{\min}$  and  $R_{\max}$  was computed. This approach enabled computation of 95% confidence intervals for the change in recruitment produced by each covariate over its historical range.

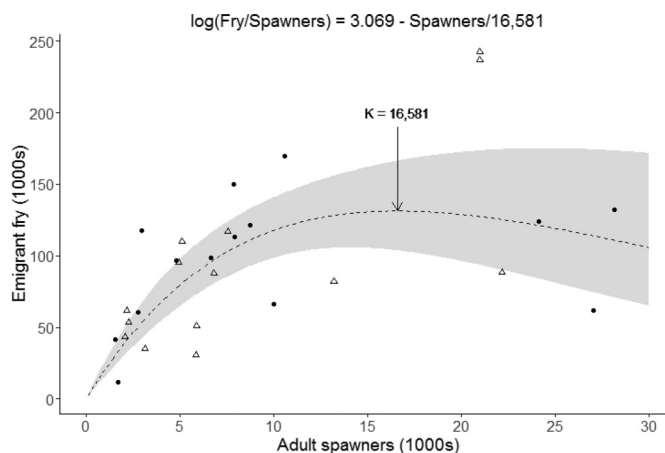
## Results

### Abundance-based models of productivity

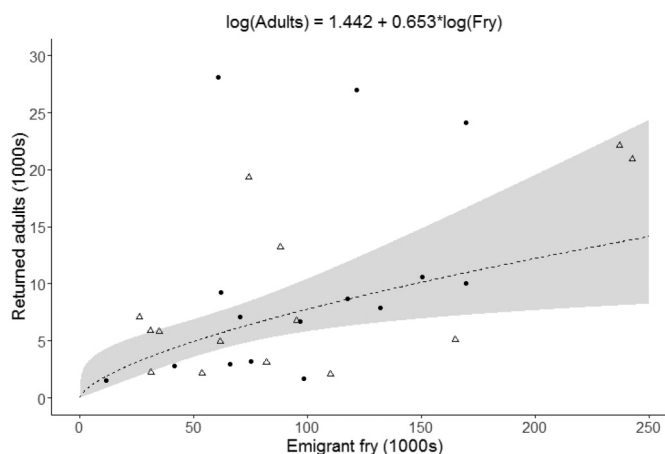
Annual censuses of Auke Creek pink salmon varied substantially over the 30 year time series; the abundance of spawning adults ranged between approximately 1500 and 28 000 and the abundance of emigrant fry ranged between 12 000 and 243 000. The abundance-based model of freshwater productivity demonstrated a positive, density-dependent relationship between the abundances of adults and emigrant fry (Fig. 4) and explained approximately half of the interannual variation in fry abundance ( $R^2 = 0.525$ ). The model estimated that the carrying capacity ( $K$ ) of Auke Creek was 16 581 adults during the time series. Individual analyses of each brood line had similar results, so the data were combined to increase power. Temporal plots of residuals from the abundance-based model did not reveal any trends of first- or second-order autocorrelation, and statistical tests of autocorrelation, performed with the “act” function in R, did not reveal any significant autoregressive coefficients through five orders.

The abundance of emigrant fry at Auke Creek exhibited a significant, positive relationship with the abundance of returned adults (Fig. 5) and explained a moderate portion of its interannual variation ( $R^2 = 0.273$ ). Individual analyses of each brood line had similar results, so the data were combined to increase power. There were no patterns of first- or second-order autocorrelation evident in plots of residuals from this model against brood years. This observation was supported by statistical tests of autocorrelation, which did not produce any significant autoregressive coefficients across five orders.

**Fig. 4.** Abundance-based model of freshwater productivity of Auke Creek pink salmon from the odd-year (circles) and even-year (triangles) brood lines ( $R^2 = 0.525$ ). The carrying capacity is denoted  $K$ . The shaded region depicts the 95% confidence interval.



**Fig. 5.** Abundance-based model of marine productivity of Auke Creek pink salmon from the odd-year (circles) and even-year (triangles) brood lines ( $R^2 = 0.273$ ). The shaded region depicts the 95% confidence interval.



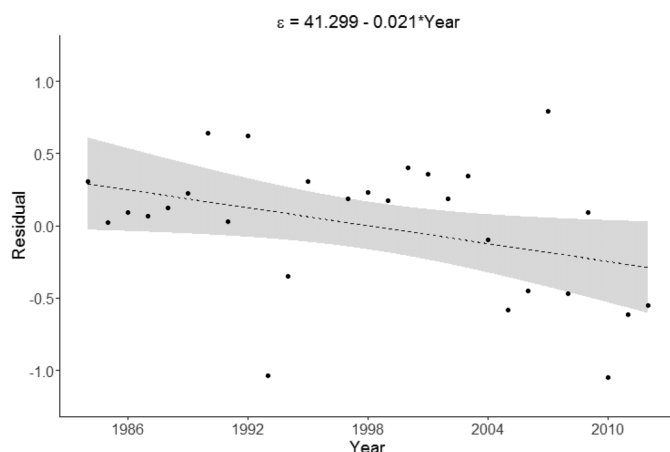
### Environmentally based model of freshwater productivity

GAMs did not reveal a significant nonlinear relationship between the residual errors and any of the environmental covariates of freshwater productivity ( $\text{edf} \sim 1$ ), so parametric linear models were used. Computation of correlation coefficients revealed moderately significant correlation ( $P < 0.10$ ) between some pairs of covariates (Appendix A, Table A4). General linear models were constructed with all possible combinations of noncorrelated covariates, and interactions were included where theory supported them (Appendix A, Table A6). The model with the lowest AIC value included the year of adult migration, which exhibited a negative linear relationship with the residual errors (Fig. 6). Comparisons of this model with the other models indicated that there were three bivariate models that had AIC values that were nearly as low. Those models, which separately included stream temperature during the adult migration period, stream flow during the adult migration period, and stream flow during the incubation period, ranged between 0.38 and 0.45 times as likely to minimize the information loss.

### Environmentally based model of marine productivity

None of the five covariates of marine productivity exhibited a nonlinear relationship with the residual errors ( $\text{edf} \sim 1$ ), so para-

**Fig. 6.** Environmentally based model of freshwater productivity of Auke Creek pink salmon ( $R^2 = 0.144$ ). The response variable was the residuals from the abundance-based model of freshwater productivity. The model included the year of adult migration. The shaded region depicts the 95% confidence interval.



metric linear models were used. Moderately significant correlations ( $P < 0.10$ ) existed between some pairs of covariates (Appendix A, Table A5), and general linear models of marine productivity were constructed with each possible combination of noncorrelated covariates (Appendix A, Table A7). The model with the lowest AIC value included sea-surface temperature during spring, which exhibited a positive linear relationship with the residual errors, and stream flow during the late-emigration period, which exhibited a negative linear relationship with the residual errors (Fig. 7). There were two other multivariate models that had AIC values that were nearly as low. Those models, which separately included Dolly Varden or coho salmon abundance as covariates in addition to stream flow and sea-surface temperature, were 0.43 and 0.60 times as probable to minimize the information loss, respectively. Sea-surface temperature and stream flow collectively explained the majority of the environmentally based variation in marine productivity ( $R^2 = 0.558$ ), and a linear model that included the abundance of emigrant fry and along with those two covariates accounted for more than two thirds of the interannual variation in adult recruitment ( $R^2 = 0.681$ ).

#### Adult recruitment simulation

Based on the most parsimonious productivity models, spawner abundance was chosen to model the freshwater component of recruitment, whereas vernal sea-surface temperature and stream flow during the late-emigration period were chosen to model the marine component. Bayesian models of the freshwater and marine components attained convergence ( $\hat{R} < 1.001$ ) and produced adequate effective sample sizes ( $>1000$ ) for each parameter. Simulated adult recruitment (Table 1) over the range of spawner abundances in the time series was smallest at the lowest spawner abundance and highest at the population carrying capacity, and the mean difference between these two estimates was approximately twofold. The 95% confidence interval of  $R_{\Delta}$  for spawner abundance was strongly positive with no overlap of zero, demonstrating a statistically significant effect on adult recruitment. The covariates of marine productivity also had large effects on adult recruitment. The mean adult recruitment level at the lowest stream flow of Auke Creek observed during the late-emigration period was more than six times as large as that estimated at the highest stream flow. Similarly, the mean adult recruitment level at the warmest vernal sea-surface temperature of Auke Bay was nearly six times larger than at the coolest temperature. This difference corresponded to an estimated increase of approximately 5000 returned adults per  $1^{\circ}\text{C}$  increase in sea-surface temperature.

The 95% confidence intervals of  $R_{\Delta}$  for stream flow and sea-surface temperature were both strongly positive with no zero overlap, demonstrating statistically significant effects of these physical drivers on adult recruitment. The 95% confidence intervals of  $R_{\Delta}$  for the marine covariates exhibited no overlap with the confidence interval for spawner abundance, thereby demonstrating that these marine covariates each had a significantly larger effect on adult recruitment than spawner abundance.

#### Discussion

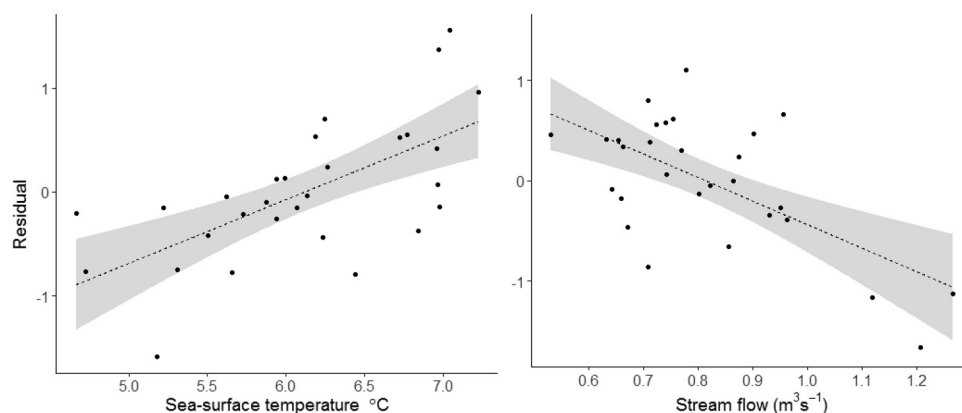
Our results suggest that density limitation controls fry production in Auke Creek. Over the 30 year time series, runs of spawning adults have averaged approximately 9500 fish and have exceeded the estimated carrying capacity in more than 20% of years. Because most of these fish spawn in a stretch of habitat less than 300 m long, competition for limited habitat probably hinders successful deposition and survival of embryos in some years. This is supported by the high levels of egg retention and redd superimposition that have been observed in association with high spawner densities in Auke Creek (Fukushima and Smoker 1997; Fukushima et al. 1998).

Because spawning habitat limits the number of fry that migrate into Auke Bay each spring, we expected that competition for resources in the nearshore environment would be minimal and that a linear model would capture the marine population dynamics effectively. While a linear model provided a reasonable fit to the data (Fig. 5), fry abundance accounted for less than a third of the variation in adult recruitment ( $R^2 = 0.273$ ), suggesting that there is substantial interannual variation in marine productivity arising from environmental factors. Some of this variation may be attributable to the commercial harvest of Auke Creek pink salmon and to straying of adults into nonnatal streams. The influence of the commercial fishery in Southeast Alaska on individual stocks is difficult to determine because the harvest is not terminal and includes mixtures of pink salmon stocks that are biologically and geographically diverse (Piston and Heintz 2011). Although harvest rates of Auke Creek pink salmon are unknown in this fishery, the total annual catch of pink salmon in northern Southeast Alaska has commonly exceeded 10 million fish and has varied substantially over the past 30 years. Estimates of straying of rates of Auke Creek pink salmon into nearby streams have ranged between 2% and 4% (Mortensen et al. 2002; Gilk et al. 2004), indicating that some natural interchange does occur among streams. Of greater concern is the effect of straying of hatchery fish into Auke Creek. Mortensen et al. (2002) estimated a straying rate of 7% for pink salmon originating from nearby Gastineau Hatchery. Because large numbers of pink salmon (2–48 million fry) were released from this hatchery from 1988 to 2002 (Stopha 2014), straying may have biased marine survival estimates during that part of the time series. However, we observed that marine survival from 1988 to 2002 (11.1%) was similar to marine survival during the rest of the time series (11.5%), suggesting that there was little systematic variation introduced by hatchery straying. Collectively, these characteristics suggest that, while commercial harvest and hatchery straying do occur, the effects of these processes on adult recruitment are more likely to be stochastic than deterministic. Hence, the ecological effects that we report here have been resolved in spite of background noise originating from these anthropogenic sources of variation.

Among the models of freshwater productivity with the lowest AIC values were two that separately included stream flow and temperature. However, because the coefficient estimates for these covariates had large standard errors and had signs that were inconsistent with expectations, there was minimal support for an influence of either of covariate on freshwater productivity. Our inability to detect effects of high temperatures or low flows was unanticipated, given that sustained stream temperatures in ex-



**Fig. 7.** Univariate plots depicting the relationship between the residuals from the abundance-based model of marine productivity and the two environmental covariates from the most parsimonious environmentally based model. Sea-surface temperatures were averaged from 15 March to 15 May to overlap the period just prior to and during the emigration, and stream flows were averaged from 1 May to 31 May to overlap the end of the emigration. The shaded regions depict the 95% confidence interval.



**Table 1.** Simulated recruitment of adult pink salmon to Auke Creek based on ecologically relevant covariates.

Covariate	Range	$R_{\min}$	$R_{\max}$	$R_{\Delta}$	Lower CI (2.5%)	Upper CI (97.5%)
Spawner abundance	1548–28 127	3752 (310)	9073 (705)	5322	3855	6789
Sea-surface temperature (°C)	4.664–7.223	3184 (187)	17 547 (1030)	14 362	12 710	16 015
Stream flow (m³ s⁻¹)	0.532–1.268	2693 (156)	17 029 (984)	14 336	12 713	15 960

**Note:** Sea-surface temperatures were averaged from 15 March to 15 May to overlap the period just prior to and during the emigration, and stream flows were averaged from 1 May to 31 May to overlap the end of the emigration. Mean simulated recruitment levels and standard errors (parentheses) are listed for the values of each covariate that minimized ( $R_{\min}$ ) and maximized ( $R_{\max}$ ) recruitment during the time series. Mean changes in recruitment ( $R_{\Delta}$ ) between those covariate values are listed with 95% confidence intervals.

cess of 15 °C have been linked to high egg retention rates in early-migrating fish (Taylor 2008a) and low flows have been linked to shortened stream life of early-migrating females, presumably because of delayed stream entry and reduced oxygen (Fukushima and Smoker 1997). While stream temperature and flow described seasonal variation of freshwater productivity in those studies, they failed to capture interannual variation in our study. A possible explanation for this is that reduced spawning success of early-migrating adults in years of poor water conditions may leave more unused spawning habitat for late-migrating adults. Under this hypothesis, gains in freshwater productivity later in the season partially offset losses in productivity earlier in the season, thereby stabilizing aggregate productivity among years.

We detected a significant, negative temporal trend in freshwater productivity over the time series (Fig. 6). Because none of the indices of stream temperature and flow exhibited a significant trend during the 30 year time series, this decline in productivity may be instead related to the quality of spawning substrate in Auke Creek. The recent history of Auke Creek provides a possible explanation for this trend. Installation of four low weirs filled with gravel in 1963 transformed much of the streambed from primarily large cobble, boulder, and bedrock to gravel substrate. These modifications improved the quality of spawning substrate within a ~1000 m² expanse of habitat that is the primary spawning ground of pink salmon. Since the improvement of the spawning beds, periodic floods have washed away substantial amounts of gravel, causing the streambed to gradually revert toward its natural state (Taylor 2008a) and reducing the quality of spawning habitat. The trend in freshwater productivity may also be related to declines in the duration of adult migrations, which have been observed in both brood lines (Kovach et al. 2012). Staggering of the use of limited habitat over the spawning season is thought to enhance the carrying capacity of this population (Gharrett et al. 2013) and, consequently, temporal compression of the adult migration may have contributed to declines in fry production.

Two of the three most parsimonious models of marine productivity included Dolly Varden or coho salmon abundance. However, the estimated coefficient of each predator abundance index had a large standard error and was positive, which was inconsistent with expectations. Hence, there was minimal support for an effect of the abundance of either predator species on survival. Our inability to detect an effect of predator abundance may be a consequence of predation from multiple species resulting in diminished effects of individual species. For instance, three sculpin species (great sculpin (*Myoxocephalus polyacanthocephalus*), Pacific staghorn sculpin (*Leptocottus armatus*), and Buffalo sculpin (*Enophrys bison*)) are also known to prey on pink salmon fry in Auke Bay (Mortensen et al. 2000). The influence of individual species may be further reduced if fry abundance buffers against predation rates (i.e., depensation).

Our observation that vernal sea-surface temperatures covaried positively with marine productivity of Auke Creek pink salmon (Fig. 7) was consistent with previous research that demonstrated a positive correlation between vernal ocean temperature and marine survival across multiple stocks and species of Pacific salmon (Mueter et al. 2005). Sea-surface temperature probably influences survival through its effects on growth. In addition to its physiological effect on growth of fry, sea-surface temperature may indirectly effect growth of fry by modulating the dynamics of their prey. For example, the abundance and size of calanoid copepods, an energetically dense food source for fry, are positively associated with water temperatures in Auke Bay (Bienfang and Ziemann 1995). Studies of tagged fry from Auke Creek have demonstrated that marine survival is correlated with growth rate (Mortensen et al. 2000), and a mechanism linking growth to survival is provided by the critical-size hypothesis (Beamish and Mahnken 2001).

Marine survival of Alaskan pink salmon stocks covaries positively with vernal freshwater input from streams, suggesting that the interaction between mixed layer conditions and plankton dynamics is an important determinant of survival (Mueter et al.

2005). Based on this, we hypothesized that high stream flows of Auke Creek in early spring would create mixed layer conditions that favor higher primary productivity in Auke Bay and, by extension, higher survival of fry. However, our analysis failed to detect an association between stream flow and marine survival. This unexpected result could be explained by plankton surveys in Auke Bay, which demonstrated that the peak phytoplankton biomass during the primary bloom always exceeds that required to saturate grazing zooplankton (Bienfang and Ziemann 1995). Those observations suggest that interannual variation in the primary plankton bloom is uncoupled from the abundance of zooplankton in this system.

In contrast, we observed that stream flow during the late-emigration period exhibited a negative association with marine survival (Fig. 7). This period is characterized by steadily increasing and highly variable stream flows (Fig. 3). High stream flows can displace river plume fronts in estuaries, which may influence marine dynamics of juvenile salmon (De Robertis et al. 2005; Burla et al. 2010). Fronts provide an interface between fresh and saline water for nearly emergent fry acclimating to the ocean and may provide feeding opportunities by concentrating zooplankton (Morgan et al. 2005). The distribution of salmon fry in estuaries likely reflects a trade-off between the protected, shallow near-shore habitat and the energetically rich offshore waters, and the presence of nearshore fronts may present an opportunity to realize the benefits of both habitats. It follows that high stream flows and resulting offshore displacement of the front could cause an unfavorable shift in the estuarine distribution of juvenile salmon. Support for this hypothesis was provided by observations in Prince William Sound, which demonstrated that dispersal of pink salmon fry to offshore waters was associated with nearshore declines in zooplankton abundance and coincided with a fivefold increase in fry mortality (Willette 2001). Tagging studies conducted in Auke Bay, which demonstrated that nearshore residence time of juvenile pink salmon from Auke Creek varied both seasonally and among brood years (Mortensen et al. 2000), produced evidence that estuarine residence patterns are linked to environmental conditions in this system. However, the determinants, characteristics, and variability of freshwater fronts in Auke Bay have not been explored in detail, and without information of this nature, this hypothesis remains untested.

Our analyses produced evidence of a greater role of habitat availability than water conditions in modulating fry production, a result that was reinforced by our observation of concurrent declines in freshwater productivity and spawning substrate quality. Spawning habitat availability may be a prominent feature of the dynamics of other salmonid populations that spawn in small coastal streams, and our results support the importance of tailoring management programs to conserve vital spawning habitat in these populations. In the marine environment, we observed strong evidence that survival is primarily determined by physical conditions that influence mortality rates of juveniles during their incipient marine residency. Moreover, our recruitment simulation demonstrated that these marine ecological factors had a comparatively larger effect on lifetime productivity than freshwater ecological factors, thereby providing compelling support for the hypothesis that brood year strength is determined by early marine survival in many salmonid populations. An important implication of this observation is that demographic processes are tightly coupled to nearshore oceanic conditions and, therefore, we would expect this stage to drive the response to climate change in many salmonid populations. Indeed, significant trends toward earlier migration times of adult and juvenile pink salmon have been observed in both brood lines at Auke Creek (Kovach et al. 2012), and these phenological changes are consistent with juveniles exploiting an earlier vernal warming period (Manhard 2016). The fact that earlier migrations are occurring in adults as fall stream temperatures become warmer (Taylor 2008b), despite a

tendency of migrating adults to delay stream entry in warmer years (Kovach et al. 2013), further suggests that this phenological response to climate change has its origins in the early marine stage.

## Acknowledgements

This manuscript represents a portion of C. Manhard's doctoral work at the University of Alaska Fairbanks. The research was sponsored by Alaska Sea Grant with funds from the National Oceanic and Atmospheric Administration Office of Sea Grant, Department of Commerce, under grant No. NA060AR4170013, project No. R/31-13, and from the University of Alaska with funds appropriated by the state.

## References

- Anas, R.E. 1959. Three-year-old pink salmon. *J. Fish. Res. Board Can.* **16**(1): 91–94. doi:10.1139/f59-010.
- Beamish, R.J., and Mahnken, C. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Prog. Oceanogr.* **49**: 423–437. doi:10.1016/S0079-6611(01)00034-9.
- Beamish, R.J., Mahnken, C., and Neville, C.M. 2004. Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. *Trans. Am. Fish. Soc.* **133**(1): 26–33. doi:10.1577/T03-028.
- Bienfang, P.K., and Ziemann, D.A. 1995. APPRISE: a multi-year investigation of environmental variation and its effects on larval recruitment. In *Climate change and northern fish populations*. Edited by R.J. Beamish. *Can. Spec. Publ. Fish. Aquat. Sci.* **121**. pp. 483–487.
- Burla, M., Baptiste, A.M., Casillas, E., Williams, J.G., and Marsh, D.M. 2010. The influence of the Columbia River plume on the survival of steelhead (*Oncorhynchus mykiss*) and Chinook salmon (*Oncorhynchus tshawytscha*): a numerical exploration. *Can. J. Fish. Aquat. Sci.* **67**(1): 1671–1684. doi:10.1139/F10-083.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information theoretic approach. Springer, New York.
- De Robertis, A., Morgan, C.A., Schabetsberger, R., Zabel, R.W., Brodeur, R.D., Emmett, R.L., Knight, C.M., Krutzikowsky, G.K., and Casillas, E. 2005. Columbia River plume fronts. II. Distribution, abundance, and feeding ecology of juvenile salmon. *Mar. Ecol. Prog. Ser.* **299**: 33–44. doi:10.3354/meps299033.
- Essington, T.E., Quinn, T.P., and Ewert, V.E. 2000. Intra- and inter-specific competition and the reproductive success of sympatric Pacific salmon. *Can. J. Fish. Aquat. Sci.* **57**(1): 205–213. doi:10.1139/f99-198.
- Farley, E.V., Murphy, J.M., Adkison, M.D., Eisner, L.B., Helle, J.H., Moss, J.H., and Nielsen, J. 2007. Early marine growth in relation to marine-stage survival rates for Alaskan sockeye salmon (*Oncorhynchus nerka*). *Fish. Bull.* **105**(1): 121–130.
- Fukushima, M. 1996. Effects of density-dependence, environment and species interaction during spawning and incubation on population dynamics of pink and sockeye salmon in the Auke Lake system, southeast Alaska. Ph.D. thesis, University of Alaska, Fairbanks, Alaska.
- Fukushima, M., and Smoker, W.W. 1997. Determinants of stream life, spawning efficiency, and spawning habitat in pink salmon in the Auke Lake system, Alaska. *Can. J. Fish. Aquat. Sci.* **54**(1): 96–104. doi:10.1139/f96-258.
- Fukushima, M., Quinn, T.J., and Smoker, W.W. 1998. Estimation of eggs lost from superimposed pink salmon (*Oncorhynchus gorbuscha*) redds. *Can. J. Fish. Aquat. Sci.* **55**(3): 618–625. doi:10.1139/f97-260.
- Gargett, A.E. 1997. The optimal stability 'window': a mechanism underlying decadal fluctuations in North Pacific salmon stocks? *Fish. Oceanogr.* **6**: 109–117. doi:10.1046/j.1365-2419.1997.00033.x.
- Gelman, A., and Rubin, D.B. 1992. Inference from iterative simulation using multiple sequences. *Stat. Sci.* **7**: 457–472. doi:10.1214/ss/1177011136.
- Gharrett, A.J., Joyce, J.E., and Smoker, W.W. 2013. Fine-scale temporal adaptation within a salmonid population: mechanism and consequences. *Mol. Ecol.* **22**: 4457–4469. doi:10.1111/mec.12400.
- Gibson, R.J., and Myers, R.A. 1988. Influence of seasonal river discharge on survival of juvenile Atlantic salmon, *Salmo salar*. *Can. J. Fish. Aquat. Sci.* **45**(2): 344–348. doi:10.1139/f88-040.
- Gilk, S.E., Wang, I.A., Hoover, C.L., Smoker, W.W., and Taylor, S.G. 2004. Outbreeding depression in hybrids between spatially separated pink salmon, *Oncorhynchus gorbuscha*, populations: marine survival, homing ability, and variability in family size. *Environ. Biol. Fishes.* **69**: 287–297. doi:10.1023/B:EBFI.0000022888.28218.c1.
- Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment. Chapman and Hall, New York.
- Kovach, R.P., Gharrett, A.J., and Tallmon, D.A. 2012. Genetic change for earlier migration timing in a pink salmon population. *Proc. R. Soc. B Biol. Sci.* **279**: 3870–3878. doi:10.1098/rspb.2012.1158.
- Kovach, R.P., Joyce, J.E., Echave, J.D., Lindberg, M.S., and Tallmon, D.A. 2013. Earlier migration timing, decreasing phenotypic variation, and biocomplexity in multiple salmonid species. *PLoS ONE*, **8**(1): e53807. doi:10.1371/journal.pone.0053807.



- Manhard, C.V. 2016. Environmental, biological, and genetic factors influencing local adaptation of pink salmon (*Oncorhynchus gorbuscha*) in Auke Creek, Alaska. Ph.D. thesis, University of Alaska, Fairbanks, Alaska.
- Montgomery, D.R., Buffington, J.M., Peterson, N.P., Schuett-Hames, D., and Quinn, T.P. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Can. J. Fish. Aquat. Sci.* 53(5): 1061–1070. doi:10.1139/f96-028.
- Morgan, C.A., De Robertis, A., and Zabel, R.W. 2005. Columbia River plume fronts. I. Hydrography, zooplankton distribution, and community composition. *Mar. Ecol. Prog. Ser.* 299: 19–31. doi:10.3354/meps299019.
- Mortensen, D.G., Wertheimer, A.C., Taylor, S.G., and Landingham, J. 2000. The relation between early marine growth of pink salmon, *Oncorhynchus gorbuscha*, and marine water temperature, secondary production, and survival to adulthood. *Fish. Bull.* 98: 319–335.
- Mortensen, D.G., Wertheimer, A.C., Maselko, J.M., and Taylor, S.G. 2002. Survival and straying of Auke Creek, Alaska, pink salmon marked with coded wire tags and thermally induced otolith marks. *Trans. Am. Fish. Soc.* 131: 14–26. doi:10.1577/1548-8659(2002)131<0014:SASOAC>2.0.CO;2.
- Moss, J.H., Beauchamp, D.A., Cross, A.D., Myers, K.W., Farley, E.V., Murphy, J.M., and Helle, J.H. 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. *Trans. Am. Fish. Soc.* 134: 1313–1322. doi:10.1577/T05-054.1.
- Mueter, F.J., Ware, D.M., and Peterman, R.M. 2002. Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the north-east Pacific Ocean. *Fish. Oceanogr.* 11(4): 205–218. doi:10.1046/j.1365-2419.2002.00192.x.
- Mueter, F.J., Pyper, B.J., and Peterman, R.M. 2005. Relationships between coastal ocean conditions and survival rates of northeast Pacific salmon at multiple lags. *Trans. Am. Fish. Soc.* 134: 105–119. doi:10.1577/T-04-033.1.
- Murphy, M.L. 1985. Die-offs of pre-spawn adult pink salmon and chum salmon in southeastern Alaska. *N. Am. J. Fish. Manage.* 5: 302–308. doi:10.1577/1548-8659(1985)5<302:DOPAPS>2.0.CO;2.
- Piston, A.W., and Heintz, S.C. 2011. Pink salmon stock status and escapement goals in Southeast Alaska. Alaska Department of Fish and Game, Special Publication No. 11–18, Anchorage, Alaska.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling.
- Plummer, M. 2016. rjags: Bayesian Graphical Models using MCMC. R package version 4–6. <https://CRAN.R-project.org/package=rjags>.
- Quinn, T.J., and Niebauer, H.J. 1995. Relation of eastern Bering Sea walleye pollock (*Theragra chalcogramma*) recruitment to environmental and oceanographic variables. *Can. Spec. Publ. Fish. Aquat. Sci.* 121. pp. 497–507.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* 11: 559–623. doi:10.1139/f54-039.
- Royer, T.C., Grosch, C.E., and Mysak, L.A. 2001. Interdecadal variability of North-east Pacific coastal freshwater and its implications on biological productivity. *Prog. Oceanogr.* 49: 95–111. doi:10.1016/S0079-6611(01)00017-9.
- Stopha, M. 2014. An evaluation of the Macaulay hatchery for consistency with statewide policies and prescribed management practices. Alaska Department of Fish and Game Regional Information Report 5J14-03.
- Taylor, S.G. 1980. Marine survival of pink salmon fry from early and late spawners. *Trans. Am. Fish. Soc.* 109: 79–82. doi:10.1577/1548-8659(1980)109<79:MSOPSF>2.0.CO;2.
- Taylor, S.G. 2008a. Auke Creek Weir 2007 annual report, operations, fish counts, and historical summaries. Unpublished report. National Marine Fisheries Service, Auke Bay Fisheries Laboratory.
- Taylor, S.G. 2008b. Climate warming causes phenological shift in pink salmon, *Oncorhynchus gorbuscha*, behavior at Auke Creek, Alaska. *Glob. Change Biol.* 14: 229–223. doi:10.1111/j.1365-2486.2007.01494.x.
- Willette, T.M. 2001. Foraging behaviour of juvenile pink salmon (*Oncorhynchus gorbuscha*) and size-dependent predation risk. *Fish. Oceanogr.* 10(1): 110–131. doi:10.1046/j.1054-6006.2001.00042.x.
- Wood, S.N. 2001. mgcv: GAMs and generalized Ridge Regression for R. *R News*, 1: 20–25.

## Appendix A

### Reconstruction of autumn stream flows of Auke Creek

Following Fukushima (1996), daily autumn stream flows of Auke Creek during the study period (1984–2012) were reconstructed with a general linear model, which was fit with stream flow and rainfall data collected from 1962 to 1975. The reconstruction of autumn stream flow was limited to the months of August–October, a period in which flow regimes vary predictably in accordance with rainfall patterns. Specifically, a power transformation was applied to daily flow rate of Auke Creek ( $F_t$ ), based on the optimal level of power ( $\lambda = 0.5$ ) selected by a Box–Cox optimization function (Box and Cox 1964), and transformed flow rate ( $B_t$ ) was modeled as a linear function of daily rainfall ( $R$ ) on the current and preceding 16 days:

$$B_t = \frac{F_t^\lambda - 1}{\lambda}$$

$$B_t = -1.75 + 0.12R_t + 0.16R_{t-1} + 0.11R_{t-2} + 0.08R_{t-3} + 0.06R_{t-4} + 0.05R_{t-5} + 0.04R_{t-6} + 0.03R_{t-7} + 0.02R_{t-8} + 0.02R_{t-9} + 0.02R_{t-10} + 0.02R_{t-11} + 0.02R_{t-12} + 0.01R_{t-13} + 0.01R_{t-14} + 0.01R_{t-15} + 0.01R_{t-16} + \varepsilon_t$$

Each of the 18 coefficients in the linear model was significant ( $P < 0.05$ ) (Table A2), and the model accounted for approximately 82% of the variation in daily stream flow in autumn during the observed time frame.

### Reconstruction of spring stream flows of Auke Creek

Daily spring stream flows of Auke Creek during the study period (1983–2011) were reconstructed with a general linear model, which was fit with environmental data collected from 1962 to 1975 including stream flow, rainfall, and air temperature. The reconstruction of spring stream flows was performed for the months of March–May, a period when melt water from snow pack accumu-

lated over the winter and ice on Auke Lake, along with rainfall, contribute to flow regimes. As was done in modeling fall stream flow, a power transformation was applied to daily flow rate of Auke Creek in spring ( $F_t$ ), based on the optimal level of power ( $\lambda = 0.1$ ) selected by a Box–Cox optimization function (Box and Cox 1964), and transformed flow rate ( $B_t$ ) was modeled as a linear function of daily rainfall ( $R$ ) on the current and preceding 15 days and temperature ( $T$ ) on the preceding 3 days:

$$B_t = \frac{F_t^\lambda - 1}{\lambda}$$

$$B_t = -9.38 + 0.02R_t + 0.03R_{t-1} + 0.02R_{t-2} + 0.02R_{t-3} + 0.02R_{t-4} + 0.01R_{t-5} + 0.01R_{t-6} + 0.01R_{t-7} + 0.01R_{t-8} + 0.01R_{t-9} + 0.01R_{t-10} + 0.01R_{t-11} + 0.01R_{t-12} + 0.01R_{t-13} + 0.01R_{t-14} + 0.01R_{t-15} + 0.002T_{t-1} + 0.001T_{t-2} + 0.003T_{t-3} + \varepsilon_t$$

Each of the 20 coefficients in the linear model was significant ( $P < 0.05$ ) (Table A3), and the model accounted for approximately

70% of the variation in daily stream flow in spring during the observed time frame.

**Table A1.** Annual counts (*N*) of pink salmon fry and adults made at the Auke Creek weir.

Brood year	Origin	Mark	Fry year	<i>N</i> <sub>fry</sub>	Adult year	<i>N</i> <sub>adults</sub>	Released
1982	Wild	None	1983	164 784 <sup>M</sup>	1984	5115 <sup>FM</sup>	Yes
	Hatchery	Adipose, ventral		20 000		77	No
	Hatchery	Adipose, CWT		19 777		79	No
1983	Wild	None	1984	169 552 <sup>M</sup>	1985	24 124 <sup>FM</sup>	Yes
	Hatchery	Adipose, CWT		87 955		1910	No
	Hatchery	Adipose, ventral		10 975		283	No
1984	Wild	None	1985	110 001 <sup>FM</sup>	1986	2089 <sup>FM</sup>	Yes
	Hatchery	Adipose, CWT		101 296		216	No
1985	Wild	None	1986	70 437 <sup>FM</sup>	1987	7117 <sup>FM</sup>	Yes
	Wild	Adipose, CWT		52 980 <sup>F</sup>		782 <sup>F</sup>	Yes
	Hatchery	Ventral		5165		12	No
1986	Wild	None	1987	26 253 <sup>FM</sup>	1988	7060 <sup>FM</sup>	Yes
	Wild	Adipose, CWT		17 249 <sup>F</sup>		508 <sup>F</sup>	Yes
	Hatchery	Ventral		16 562		572	No
1987	Wild	None	1988	74 912 <sup>FM</sup>	1989	3160 <sup>FM</sup>	Yes
	Wild	Adipose, CWT		38 149 <sup>F</sup>		1635 <sup>F</sup>	Yes
	Hatchery	Ventral		66 376		1545	No
1988	Wild	None	1989	74 170 <sup>FM</sup>	1990	19 382 <sup>FM</sup>	Yes
	Wild	Adipose, CWT		42 700 <sup>F</sup>		1601 <sup>F</sup>	Yes
	Hatchery	Ventral		38 976		777	No
1989	Wild	None	1990	96.651 <sup>FM</sup>	1991	6653 <sup>FM</sup>	Yes
	Hatchery	Ventral		80 014		225	No
1990	Wild	None	1991	242 772 <sup>FM</sup>	1992	20 972 <sup>FM</sup>	Yes
	Hatchery	Ventral		64 137		1127	No
1991	Wild	None	1992	98 449 <sup>FM</sup>	1993	1688 <sup>FM</sup>	Yes
	Hatchery	Adipose		29 086		8	No
1992	Wild	None	1993	237 073 <sup>FM</sup>	1994	22 167 <sup>FM</sup>	Yes
	Hatchery	Adipose		22 879		361	No
1993	Wild	None	1994	11 603 <sup>FM</sup>	1995	1548 <sup>FM</sup>	Yes
1994	Wild	None	1995	43 632	1996	1288	Yes
	Wild	Adipose, CWT		44 270		68	No
	Hatchery	Otolith		633 147		2763	Yes
	Hatchery	Adipose, CWT		116 745		222	No
	Hatchery	Adipose, ventral		24 697		78	No
1995	Wild	None	1996	41 359 <sup>FM</sup>	1997	2774 <sup>FM</sup>	Yes
1996	Wild	None	1997	31 092 <sup>FM</sup>	1998	2267 <sup>FM</sup>	Yes
	Hatchery	Adipose, ventral		40 764		608	No
1997	Wild	None	1998	60 785 <sup>FM</sup>	1999	28 127 <sup>FM</sup>	Yes
	Hatchery	Adipose, ventral		39 834		1853	No
1998	Wild	None	1999	53 533 <sup>FM</sup>	2000	2181 <sup>FM</sup>	Yes
	Hatchery	Adipose, ventral		40 074		301	No
1999	Wild	None	2000	132 075 <sup>FM</sup>	2001	7857 <sup>FM</sup>	Yes
	Hatchery	Adipose, ventral		40 000		448	No
2000	Wild	None	2001	61 504 <sup>FM</sup>	2002	4928 <sup>FM</sup>	Yes
2001	Wild	None	2002	150 149 <sup>FM</sup>	2003	10 580 <sup>FM</sup>	Yes
2002	Wild	None	2003	95 132 <sup>FM</sup>	2004	6802 <sup>FM</sup>	Yes
2003	Wild	None	2004	169 568 <sup>FM</sup>	2005	10 010 <sup>FM</sup>	Yes
2004	Wild	None	2005	87 928 <sup>FM</sup>	2006	13 198 <sup>FM</sup>	Yes
2005	Wild	None	2006	65 894 <sup>FM</sup>	2007	2944 <sup>FM</sup>	Yes
	Hatchery	Adipose, ventral		44 728		179	No
2006	Wild	None	2007	81 899 <sup>FM</sup>	2008	3135 <sup>FM</sup>	Yes
	Hatchery	Adipose, ventral		35 159		112	No
2007	Wild	None	2008	117 591 <sup>FM</sup>	2009	8719 <sup>FM</sup>	Yes
	Hatchery	Adipose, ventral		49 806		826	No
2008	Wild	None	2009	34 847 <sup>FM</sup>	2010	5851 <sup>FM</sup>	Yes
	Hatchery	Adipose, ventral		40 931		552	No
2009	Wild	None	2010	121 639 <sup>FM</sup>	2011	26 999 <sup>FM</sup>	Yes
2010	Wild	None	2011	30 924 <sup>FM</sup>	2012	5890 <sup>FM</sup>	Yes
2011	Wild	None	2012	61 802 <sup>FM</sup>	2013	9231 <sup>M</sup>	Yes
2012	Wild	None	2013	51 191 <sup>F</sup>	2014		

**Note:** Separate counts are listed for fish that were naturally spawned and those that were reared at the Auke Creek experimental hatchery and released into the stream. Superscripts "F" and "M" denote whether annual counts were used as input data for the freshwater or marine productivity models, respectively. CWT, coded wire tag.

**Table A2.** Summary statistics from the linear model of daily stream flow of Auke Creek in autumn as a function of rainfall lagged up to 16 days.

Term	Coefficient	SE	<i>t</i>	<i>P</i>
Intercept	-1.7510	0.0082	-213.8240	$<2 \times 10^{-16}$
$R_t$	0.1157	0.0044	26.2990	$<2 \times 10^{-16}$
$R_{t-1}$	0.1607	0.0046	35.0060	$<2 \times 10^{-16}$
$R_{t-2}$	0.1116	0.0046	24.3640	$<2 \times 10^{-16}$
$R_{t-3}$	0.0765	0.0046	16.6830	$<2 \times 10^{-16}$
$R_{t-4}$	0.0603	0.0046	13.1630	$<2 \times 10^{-16}$
$R_{t-5}$	0.0472	0.0046	10.2970	$<2 \times 10^{-16}$
$R_{t-6}$	0.0393	0.0046	8.5690	$<2 \times 10^{-16}$
$R_{t-7}$	0.0340	0.0046	7.4210	$1.97 \times 10^{-13}$
$R_{t-8}$	0.0244	0.0046	5.3460	$1.04 \times 10^{-7}$
$R_{t-9}$	0.0209	0.0046	4.5690	$5.32 \times 10^{-6}$
$R_{t-10}$	0.0193	0.0046	4.2090	$2.72 \times 10^{-5}$
$R_{t-11}$	0.0175	0.0046	3.8080	0.0001
$R_{t-12}$	0.0159	0.0046	3.4560	0.0006
$R_{t-13}$	0.0126	0.0046	2.7480	0.0061
$R_{t-14}$	0.0091	0.0046	1.9790	0.0480
$R_{t-15}$	0.0117	0.0046	2.5340	0.0114
$R_{t-16}$	0.0130	0.0044	2.9560	0.0032

**Note:** Rainfall is denoted "R" followed by the number of lagged days (e.g.,  $R_{t-5}$  corresponds to the total daily rainfall from 5 days prior).

**Table A3.** Summary statistics from the linear model of daily stream flow of Auke Creek in spring as a function of rainfall (*R*) lagged up to 15 days and temperature (*T*) lagged up to 3 days.

Term	Coefficient	SE	<i>t</i>	<i>P</i>
Intercept	-9.4194	0.0078	-1202.34	$<2 \times 10^{-16}$
$R_t$	0.019	0.0036	5.323	$1.24 \times 10^{-7}$
$R_{t-1}$	0.0264	0.0037	7.118	$1.99 \times 10^{-12}$
$R_{t-2}$	0.0232	0.0037	6.227	$6.80 \times 10^{-10}$
$R_{t-3}$	0.0218	0.0037	5.837	$7.00 \times 10^{-9}$
$R_{t-4}$	0.0187	0.0037	5.017	$6.14 \times 10^{-7}$
$R_{t-5}$	0.0138	0.0037	3.697	0.0003
$R_{t-6}$	0.0131	0.0037	3.502	0.0005
$R_{t-7}$	0.0111	0.0038	2.951	0.0032
$R_{t-8}$	0.0094	0.0037	2.526	0.0117
$R_{t-9}$	0.0107	0.0037	2.894	0.0039
$R_{t-10}$	0.0092	0.0037	2.508	0.0123
$R_{t-11}$	0.0089	0.0037	2.417	0.0158
$R_{t-12}$	0.0072	0.0037	1.943	0.0522
$R_{t-13}$	0.0089	0.0038	2.33	0.0200
$R_{t-14}$	0.0086	0.0039	2.221	0.0266
$R_{t-15}$	0.0086	0.0038	2.283	0.0227
$T_{t-1}$	0.0025	0.0005	5.373	$9.49 \times 10^{-8}$
$T_{t-2}$	0.0011	0.0006	1.827	0.0679
$T_{t-3}$	0.0032	0.0005	6.841	$1.31 \times 10^{-11}$

**Table A4.** Correlation coefficients for each pair of covariates evaluated in the environmentally based models of freshwater productivity.

	<i>Y</i>	<i>M</i>	$T_E$	$F_E$	$F_I$
<i>Y</i>	1.000				
<i>M</i>	-0.33*	1.000			
$T_E$	0.22	-0.22	1.000		
$F_E$	0.21	0.20	-0.61*	1.000	
$F_I$	0.00	0.13	-0.33*	0.21	1.000

**Note:** Covariates include adult migration year (*Y*), median date of migration (*M*), temperature during the early spawning period ( $T_E$ ), and stream flow during the early spawning ( $F_E$ ) and incubation ( $F_I$ ) periods. Asterisks indicate moderately significant values ( $P < 0.10$ ).

**Table A5.** Correlation coefficients for each pair of covariates evaluated in the abundance-based models of marine productivity.

	<i>Y</i>	<i>M</i>	<i>C</i>	<i>D</i>	$T_S$	$F_S$	$F_L$
<i>Y</i>	1.000						
<i>M</i>	-0.07	1.000					
<i>C</i>	-0.19	0.61*	1.000				
<i>D</i>	-0.23	0.31*	0.36*	1.000			
$T_S$	-0.25	-0.43*	0.20	-0.04	1.000		
$F_S$	-0.40*	-0.17	0.22	0.20	0.36*	1.000	
$F_L$	-0.41*	-0.05	0.11	0.25	0.25	0.36*	1.000

**Note:** Covariates include juvenile emigration year (*Y*), median date of emigration (*M*), coho salmon smolt (*C*) and Dolly Varden charr (*D*) abundance, sea-surface temperature during spring ( $T_S$ ), and stream flow during spring ( $F_S$ ) and during the late emigration period ( $F_L$ ). Asterisks indicate moderately significant values ( $P < 0.10$ ).



**Table A6.** Coefficients and standard errors (parentheses) of terms tested in freshwater productivity models.

AIC	$P_R$	$R^2$	Y	M	$T_E$	$F_E$	$F_I$	Interaction
38.135		0.144	-0.021 (0.010)					
39.743	0.448	0.155	-0.019 (0.010)			-0.120 (0.203)		
39.856	0.423	0.152	-0.021 (0.010)				-0.182 (0.364)	
40.070	0.380	0.146	-0.021 (0.010)		0.016 (0.065)			
41.493	0.187	0.034				-0.200 (0.208)		
41.576	0.179	0.160	-0.020 (0.010)			-0.104 (0.211)	-0.143 (0.378)	
41.800	0.160	0.024		0.011 (0.014)				
42.224	0.129	0.009					-0.186 (0.386)	
42.429	0.117	0.002			-0.013 (0.067)			
43.081	0.084	0.049		0.009 (0.015)		-0.173 (0.215)		
43.418	0.071	0.037		0.012 (0.014)			-0.229 (0.391)	
43.799	0.059	0.024		0.011 (0.015)	-0.002 (0.069)			
43.856	0.057	0.089		-0.012 (0.025)		-13.831 (13.186)		0.059 (0.057)
44.893	0.034	0.055		0.010 (0.015)		-0.152 (0.225)	-0.164 (0.407)	
45.053	0.031	0.049		0.120 (0.136)	1.542 (1.919)			-0.007 (0.008)

**Note:** Covariates include adult migration year (Y), median date of migration (M), stream temperature during the early spawning period ( $T_E$ ), and stream flow during the early spawning ( $F_E$ ) and incubation ( $F_I$ ) periods. Models are sorted by descending likelihood of being the most parsimonious ( $P_R$ ).

**Table A7.** Coefficients and standard errors (parentheses) of terms from general linear models of marine survival.

AIC	$P_R$	$R^2$	Y	M	C	D	$T_S$	$F_S$	$F_L$
48.228		0.558					0.659 (0.141)		-2.517 (0.577)
49.238	0.604	0.573			0.070 (0.075)		0.636 (0.144)		-2.550 (0.579)
49.936	0.426	0.563				0.031 (0.062)	0.667 (0.144)		-2.600 (0.608)
62.174	0.001	0.234					0.508 (0.177)		
63.822	<0.001	0.242			0.050 (0.098)		0.490 (0.183)		
63.87	<0.001	0.242				-0.041 (0.078)	0.504 (0.179)		
63.906	<0.001	0.187							-1.856 (0.744)
63.978	<0.001	0.24			0.130 (0.097)				-1.960 (0.738)
64.826	<0.001	0.217		-0.018 (0.018)					-1.891 (0.745)
65.906	<0.001	0.187				-0.001 (0.083)			-1.854 (0.783)
68.945	<0.001	0.033			0.102 (0.107)				
69.027	<0.001	0.030	0.014 (0.016)						
69.243	<0.001	0.023		-0.016 (0.020)					
69.471	<0.001	0.015						-0.998 (1.542)	
69.566	<0.001	0.012				-0.050 (0.087)			
70.086	<0.001	0.061			0.124 (0.110)			-1.391 (1.573)	
70.554	<0.001	0.046		-0.019 (0.021)				-1.242 (1.570)	
71.25	<0.001	0.023				-0.040 (0.090)		-0.853 (1.599)	

**Note:** Covariates include juvenile outmigration year (Y), median date of outmigration (M), coho salmon smolt (C) and Dolly Varden charr (D) abundance, Auke Bay sea-surface temperature during spring ( $T_S$ ), and Auke Creek stream flow during spring ( $F_S$ ) and during the late emigration period ( $F_L$ ). Models are sorted by descending likelihood of being the most parsimonious ( $P_R$ ).

## References

- Box, G.E.P., and Cox, D.R. 1964. An analysis of transformations. *J. R. Stat. Soc. Ser. B*, 26: 211–252.
- Fukushima, M. 1996. Effects of density-dependence, environment and species interaction during spawning and incubation on population dynamics of pink

and sockeye salmon in the Auke Lake system, southeast Alaska. Ph.D. thesis, University of Alaska, Fairbanks, Alaska.