

Low productivity of Chinook salmon strongly correlates with high summer stream discharge in two Alaskan rivers in the Yukon drainage

Jason R. Neuswanger, Mark S. Wipfli, Matthew J. Evenson, Nicholas F. Hughes, and Amanda E. Rosenberger

Abstract: Yukon River Chinook salmon (*Oncorhynchus tshawytscha*) populations are declining for unknown reasons, creating hardship for thousands of stakeholders in subsistence and commercial fisheries. An informed response to this crisis requires understanding the major sources of variation in Chinook salmon productivity. However, simple stock–recruitment models leave much of the variation in this system’s productivity unexplained. We tested adding environmental predictors to stock–recruitment models for two Yukon drainage spawning streams in interior Alaska — the Chena and Salcha rivers. Low productivity was strongly associated with high stream discharge during the summer of freshwater residency for young-of-the-year Chinook salmon. This association was more consistent with the hypothesis that sustained high discharge negatively affects foraging conditions than with acute mortality during floods. Productivity may have also been reduced in years when incubating eggs experienced major floods or cold summers and falls. These freshwater effects — especially density dependence and high discharge — helped explain population declines in both rivers. They are plausible as contributors to the decline of Chinook salmon throughout the Yukon River drainage.

Résumé : Les populations de saumons quinnats (*Oncorhynchus tshawytscha*) du fleuve Yukon sont en baisse pour des raisons inconnues, ce qui entraîne une situation difficile pour des milliers de parties prenantes des pêches de subsistance et commerciales. Une réponse éclairée à cette crise requiert la compréhension des grandes sources de variation de la productivité du saumon quinnat. Les modèles simples de recrutement aux stocks n’arrivent toutefois pas à expliquer une bonne partie des variations de productivité dans ce système. Nous avons testé la pertinence d’ajouter des variables environnementales prédictives aux modèles de recrutement aux stocks pour deux cours d’eau de frai du bassin versant du fleuve Yukon dans l’intérieur de l’Alaska, les rivières Chena et Salcha. Une faible productivité était fortement associée à des débits élevés durant l’été de la résidence en eau douce des saumons quinnats de l’année. Cette association correspondait mieux à l’hypothèse selon laquelle un débit élevé soutenu a une incidence négative sur les conditions d’approvisionnement qu’avec l’hypothèse d’une mortalité aiguë durant les crues. Il se peut aussi qu’une réduction de la productivité ait eu lieu durant des années où les œufs en incubation ont été exposés à de grandes crues ou des étés et automnes froids. Ces effets associés au milieu d’eau douce, particulièrement la dépendance sur la densité et les débits élevés, contribuent à expliquer les baisses des populations dans les deux rivières. Il s’agit de facteurs plausibles du déclin du saumon quinnat dans tout le bassin versant du fleuve Yukon. [Traduit par la Rédaction]

Introduction

The Yukon River Chinook salmon (*Oncorhynchus tshawytscha*) population historically supported commercial and subsistence fisheries harvesting over 140 000 fish annually (Evenson et al. 2009). It is a culturally and economically crucial resource for communities in parts of Alaska and Canada (ADF&G Chinook Salmon Research Team 2013) where other economic and subsistence opportunities may be limited by remoteness. In most years since 1998, the abundance of Chinook salmon in this drainage has been low compared with historical averages (Evenson et al. 2009), similar to patterns in many drainages throughout Alaska (ADF&G

Chinook Salmon Research Team 2013). Harvest restrictions prompted by declining stocks have caused severe hardship for thousands of stakeholders in commercial and subsistence fisheries. This problem has elicited disaster declarations and nationwide media attention (Milkowski 2009). Despite commercial fishery closures and restriction of subsistence harvest to levels below the “amount necessary for subsistence” (as designated by the Alaska Board of Fisheries), escapement up the Yukon River into Canada has failed in recent years to reach the minimum required by international treaty (Schindler et al. 2013). An informed response to this crisis requires that we identify the major drivers of salmon productivity in these systems.

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To facilitate management decisions and investigate population trends, the dynamics of salmon populations can be summarized using stock–recruitment models (Quinn and Deriso 1999) that relate the estimated spawning stock in each brood year (the number of adult fish, of mixed age, that escape the fishery to spawn in that year; i.e., escapement) with the number of recruits produced (the total number of offspring from that brood year that eventually returned, over multiple years, to be harvested or spawn themselves). The ratio of recruits per spawner in a given brood year, termed “productivity,” must be at least one for the spawners to fully replace themselves.

Commonly used stock–recruitment models such as the Ricker (1954) model describe the productivity of a population using a constant “productivity parameter” and one or more “density dependence” parameters, which represent the effects of intraspecific competition and any other mechanisms by which the number of spawners affects the number of recruits per spawner. These models often leave a large portion of the variation in productivity unexplained. For the stream-type Chinook salmon of the Yukon River drainage, the unexplained variation might be attributed to any of the natural and anthropogenic factors affecting stream-type fish in freshwater streams during their first year, in estuarine or near-shore ocean habitats during their second year, in the offshore ocean environment thereafter, or in the rivers hosting their long-distance migrations as smolts and returning spawners.

Processes acting on juvenile Pacific salmon during their freshwater residency can determine much of the variation in productivity. A review of published records found that the proportion of variation in total mortality due to fresh water ranges from 43% to 76% for most Pacific salmon species (Bradford 1995). A large proportion of the total variation in productivity can be determined by freshwater factors even if mortality during other life cycle stages is high, provided mortality during other stages is relatively constant. For example, from 2003 to 2007 the Bering–Aleutian Salmon International Survey (Farley et al. 2009) sampled juvenile Yukon drainage Chinook salmon during the juveniles’ first few months in the Bering Sea. By comparing their early marine abundance estimate for Canadian-origin juveniles with eventual adult returns, they estimated that only 6% of early marine juveniles survived to the point of recruitment; however, despite this low marine survival rate, juvenile abundance was highly correlated ($r = 0.89$) with the eventual recruitment of their brood year (Murphy et al. 2013). This correlation supports the applicability to Yukon River Chinook salmon of the working hypothesis that the majority of variation in recruitment occurs during critical periods in fresh water (Elliott 1989; Bradford 1995) or early marine entry (Beamish and Mahnken 2001).

The density-independent variables of stream discharge and temperature are also important determinants of salmonid productivity because of their substantial ecological and physiological effects. Temperature controls the rate of development and emergence times of juveniles from spawning grounds (From and Rasmussen 1991), and it mediates the relationship among food consumption, growth, and body condition (Elliott and Hurley 1999). Patterns in stream discharge affect salmonids in diverse ways. Water that is flowing faster, is more turbid, or carries more debris than normal may reduce foraging success in sight-feeding fishes (O’Brien and Showalter 1993; Piccolo et al. 2008; Neuswanger et al. 2014). Turbidity associated with high discharge inhibits primary production (Benson et al. 2013). Large floods can kill incubating embryos in the spawning gravel (Healey 1991; DeVries 1997) or displace fry from desirable habitats (Ottaway and Clarke 1981). However, moderately high discharge also creates more wetted habitat for primary productivity and occupation by fishes, and high-discharge events can entrain more invertebrate prey for fish (Gibbins et al. 2007).

Because the potential effects of discharge and temperature are so diverse, understanding how they affect a particular salmon run requires direct study of that population or representative sub-populations. In this study, we examine the effects of stream discharge and other environmental factors on Chinook salmon productivity in the Chena and Salcha rivers, tributaries of the Tanana River in the Yukon River drainage in central Alaska. Specifically, we sought to (i) test the relationship between stream discharge and productivity, (ii) determine whether the discharge–productivity relationship is sensitive to the choice of a specific discharge statistic or time period, (iii) determine whether the relationship explains the decline in Chinook salmon productivity in the Chena and Salcha rivers, and (iv) search for other relationships with discharge and temperature during both the spawning and rearing periods. We integrate our findings with those of previous ecological studies on the Chena River to identify the most plausible mechanisms behind a discharge–productivity relationship and to identify priorities for new research on both population dynamics and ecological mechanisms affecting individual fish directly.

Methods

Study rivers

We analyzed 20 years (1986–2005) of Chinook salmon stock–recruitment data for the Chena River and 19 years (1987–2005) for the Salcha River. These were the only individual spawning streams in the Yukon River drainage for which data were available for long-term run reconstructions. These fifth-order tributaries of the glacial Tanana River in interior Alaska lie in geographically similar, adjacent watersheds, and they join the Tanana River 56 km apart (WGS84 coordinates 64°47′52″N, 147°54′43″W for the Chena River outlet, and 64°29′15″N, 146°59′13″W for the Salcha River outlet). Median discharge during the open-water season (specifically, the median of the values from 1986 to 2006 of the annual median of the daily mean discharge values from 26 April to 30 September) was 47 m³·s⁻¹ near the mouth of the Chena River (at USGS gaging station 15514000 at Fairbanks) and 59 m³·s⁻¹ near the mouth of the Salcha River (station number 15484000 near Salchaket). We developed stock–recruitment models using the Chena River data, and we tested the same models in a strictly confirmatory analysis of the Salcha River data. However, data for the Salcha River were not completely independent of those for the Chena River because of the proximity of the rivers, the similarity of their watersheds, and the fact that the nonrecreational harvest portions of their recruitment estimates were both proportional to a single, middle-Yukon harvest estimate that could not be resolved to the level of individual-river stocks.

Salmon run reconstructions

Available estimates of in-river harvest, spawner abundance (also termed escapement), and spawner age composition were used to generate age-structured run reconstructions — paired estimates of spawning stock from each brood year and the number of recruits they produced (Table 1). Escapement of adult Chinook salmon was estimated annually in the Chena River from 1986 through 2010 and in the Salcha River from 1987 through 2010 using either mark–recapture or counting tower techniques (Savereide 2012). Mark–recapture estimates in the Chena River were thought to underestimate total escapement; therefore, all mark–recapture estimates were increased by a factor of 1.24 based on a single-year calibration (ratio of the two estimates) in 1997 when both methods were used (Stuby and Evenson 1998). Age compositions of the escapements were estimated annually in each river from scale samples collected from carcasses recovered from spawning grounds.

Commercial and subsistence fishing occur on a mixture of spawning stocks in the mainstem Yukon and Tanana rivers as

Table 1. Chinook salmon run reconstructions for the Chena River (1986–2005) and Salcha River (1987–2005).

Brood year	Chena		Salcha	
	Spawners	Recruits	Spawners	Recruits
1986	9 065	13 584	—	—
1987	6 404	11 029	4 771	13 416
1988	3 346	23 751	4 322	28 185
1989	2 730	31 294	3 294	34 860
1990	5 603	6 854	10 728	8 260
1991	3 172	18 259	5 608	28 827
1992	5 580	5 068	7 862	6 474
1993	12 241	19 507	10 007	18 382
1994	11 877	5 532	18 399	5 840
1995	11 394	8 941	13 643	13 653
1996	7 153	12 044	7 570	14 027
1997	13 390	11 236	18 514	14 553
1998	4 745	20 837	5 027	33 432
1999	6 485	7 381	9 198	10 297
2000	4 694	8 510	4 595	16 492
2001	9 696	8 025	13 328	20 459
2002	6 967	4 474	9 000	8 130
2003	11 100	9 739	15 500	15 996
2004	9 645	3 581	15 761	7 275
2005	4 075	7 753	5 988	24 779

Note: The number of spawners each brood year equals escapement that year, and the number of recruits produced each brood year equals total in-river harvest plus escapement over the lifespan of the cohort. (Source: Alaska Department of Fish and Game.)

Chinook salmon are en route to their spawning grounds. Total annual commercial harvests by fishing district were estimated from mandatory returns of fish tickets and were considered censuses of total harvest. Subsistence harvests by district were determined from household surveys and were considered a census of total harvest. Age compositions of the commercial and subsistence catches were determined from analysis of scales collected from a sample of the harvest in each district. Identification of specific spawning stocks in the commercial and subsistence harvest was not possible. However, scale pattern analysis was used from 1986 to 2003, and genetic methods have been used since 2004 to identify run of origin from the commercial and subsistence catch (e.g., Dubois et al. 2009). Runs were identified as lower (below river kilometre 1000), middle (between river kilometre 1000 and 2000), and upper (above river kilometre 2000) river stocks. Chinook salmon bound for the Chena and Salcha rivers comprise a portion of the middle run harvest in each fishing district.

Small recreational fisheries occur in the lower 3 km of the Salcha River and in the lower 72 km of the Chena River. Estimates of total annual recreational harvest in these rivers are obtained through an annual statewide mail-out harvest survey (e.g., Jennings et al. 2010). Age and sex composition of the recreational harvest is not known. Since 1986, annual harvests of Chinook salmon have ranged from 39 to 1280 fish in the Chena River and 47 to 1448 fish in the Salcha River. To estimate age-specific harvest in each river, we assumed age composition of the recreational harvest was equivalent to that of escapement.

We could not directly estimate the proportion of middle-run harvest by commercial and subsistence fishers that was composed of Chinook salmon from the Chena and Salcha rivers. Results from a 3-year Yukon River Chinook salmon radiotelemetry study estimated that fish heading upstream to the Chena and Salcha rivers comprised a mean of 0.427 of middle-run stocks present in the lower Yukon River during 2002–2004 (Eiler et al. 2004, 2006a, 2006b). This proportion was used to apportion middle-run harvest to Chena and Salcha river stocks for all years in the data set. Harvest was further apportioned to Chena or Salcha river stocks for each age class each year based on the relative proportional

escapement of each stock (e.g., ratio of Chena River escapement in year y to Chena River plus Salcha River escapement in year y).

Complete recruitment estimates (for ages 3–8) were available for years 1986–2002 for the Chena River and 1987–2002 for the Salcha River. For age 8 fish from the 2003 brood year, ages 7–8 fish from the 2004 brood year, and ages 6–8 fish from the 2005 brood year, recruitment was extrapolated from (a) the mean proportion of fish returning at each age in past years and (b) the known returns (in previous years) of younger fish from each brood year.

Recruitment of each age class from a given brood year was estimated as the sum of escapement ($\hat{N}_{a,y+a}$) by age, the river's estimated portion of middle-run harvest ($\hat{H}_{\text{midrun},a,y+a}$) by age, and sport harvest ($\hat{H}_{\text{sport},a,y+a}$) by age within a calendar year:

$$(1) \quad \hat{R}_{a,y} = \hat{N}_{a,y+a} + \hat{H}_{\text{sport},a,y+a} + \hat{H}_{\text{midrun},a,y+a}$$

where y denotes year class (year), a denotes age (years), and $y + a$ is the calendar year. Total recruitment for each year class in the data set was estimated as the sum of recruitment over all age classes:

$$(2) \quad \hat{R}_y = \sum_{a=3}^8 \hat{R}_{a,y}$$

Stream discharge and temperature data sources

We calculated environmental variables from publically available stream discharge and temperature records, including daily discharge data from online records of USGS hydrographs on both the Chena River near Two Rivers (station number 15493000) and the Salcha River near Salchaket (station number 15484000). To estimate daily mean water temperature from 1986 to 2006, we used the only available water temperature records from the same gaging station on the Chena River (2007 to 2011) to parameterize a nonlinear regression predicting daily mean water temperature from the daily mean air temperature at Fairbanks International Airport. This air temperature was obtained online from the NOAA National Climatic Data Center's Global Summary of the Day database (<http://www7.ncdc.noaa.gov/CDO/cdoselect.cmd?datasetabbv=GSOD>) for station ID 70261026411. Water temperature was most strongly correlated with the previous day's air temperature ($r = 0.86$; time lags of 0–4 days were examined). We used a nonlinear regression model (van Vliet et al. 2011) developed for predicting river water temperature T_{water} from air temperature T_{air} and stream discharge; however, the stream discharge term did not improve the model's explanatory power enough to justify an extra parameter, so we excluded it in a simplified model:

$$(3) \quad T_{\text{water}} = \mu + \frac{\alpha - \mu}{1 + e^{\gamma(\beta - T_{\text{air}})}} + \varepsilon, \text{ where } \gamma = \frac{4 \text{ Tan}\theta}{\alpha - \mu}$$

The lower bound on water temperature was $\mu = 0$ °C. The fixed parameters $\alpha = 11.45$, $\theta = 0.5524$, and $\beta = 11.86$ were estimated from the historical data, and ε represented random error. This relationship explained most of the variation in water temperature ($R^2 = 0.95$), with the greatest discrepancies during ice-out. Separate water temperature data were not available for the Salcha River, so we assumed it was the same as in the nearby Chena River.

Stock-recruitment models and environmental predictors

We used generalized versions of the Ricker (1954) stock-recruitment model to investigate patterns of productivity in relation to several measures of stream discharge and temperature. We present detailed results from three variants of the model: (1) the “basic model,” meaning the original Ricker model; (2) the “discharge model,” which was used for confirmatory analysis of an a priori hypothesis that poor recruitment is associated with high stream discharge during the summer the juveniles spent in fresh water;

Table 2. Variables evaluated in generalized Ricker models for Chena and Salcha river Chinook salmon.

Variable	Year	Period	Chena	Salcha	Description
-S	Brood	—	0.99999	0.99997	Number of spawners (parents) in a brood year
DISCH	Brood + 1	26 Apr. – 30 Sept.	0.999754	0.976167	Indicator variable equal to 0 when discharge was high during the summer growing season and 1 when discharge was low; the threshold between high and low was a fitted parameter
INCTMP	Brood	20 July – 25 Oct.	0.796958	0.315757	Temperature (degree-days) during the spawning and incubation period
INCFLD	Brood	20 July – 25 Oct.	0.34717	0.10899	Maximum flood peak during the spawning and incubation period
SUMFLD	Brood + 1	26 Apr. – 30 Sept.	0.327366	0.214724	Maximum flood peak during the summer growing season
EMGFLSH	Brood + 1	15 May – 15 June	0.265704	0.183761	Flashiness during the critical emergence period
FLDFRE	Brood + 1	26 Apr. – 30 Sept.	0.157909	0.189318	Number of floods exceeding seven times the long-term median summer discharge
SUMFLSH	Brood + 1	26 Apr. – 30 Sept.	0.117426	0.094218	Flashiness during the summer growing season
FLDDUR	Brood + 1	26 Apr. – 30 Sept.	0.111235	0.451539	Mean duration (days) of floods exceeding seven times the median summer discharge
EMGTMP	Brood + 1	15 May – 15 June	0.102561	0.254221	Temperature (degree-days) during the critical emergence period
EMGFLD	Brood + 1	15 May – 15 June	0.0865573	0.104117	Maximum flood peak during the critical emergence period
SUMTMP	Brood + 1	26 Apr. – 30 Sept.	0.0774589	0.092464	Degree-days during the summer growing season

Note: The “Chena” and “Salcha” columns list the total Akaike weights of all models containing each variable for each river in the full exploratory analysis.

and (3) the “full model,” the version most strongly favored by an objective model selection process in an exploratory analysis of the Chena River data using the 12 possible predictors listed in Table 2.

The basic model related recruits R to spawners S , with fitted parameters α representing productivity (recruits per spawner) in the absence of density dependence, β representing the magnitude of density dependence, and random error ε .

$$(4) \quad R = \alpha S e^{-\beta S} e^{\varepsilon}$$

Environmental predictors were represented as additional terms in the exponent of the model, following the description of the “generalized Ricker model” in Quinn and Deriso (1999):

$$(5) \quad R = \alpha S e^{-\beta S + \gamma_i X_i} e^{\varepsilon}$$

Here, X_i represents the value of the i th environmental predictor, and γ_i is the fitted parameter scaling its effect on the model.

The discharge model incorporated one environmental predictor, an indicator variable equal to 0 when discharge was high during the summer growing season and 1 when discharge was low. The summer growing season was defined a priori to extend from 26 April (mean date of spring breakup from 1968 to 2010 on the Chena River) to 30 September (an approximation of when the Chena River begins to freeze, based on personal field observations). The threshold separating high- and low-discharge years, selected by graphical examination of the residuals from the basic model, was counted as an additional fitted parameter occupying one degree of freedom in calculations of model quality measures. This threshold allows the model to approximate a sigmoid relationship with one less parameter, reducing the risk of overfitting. Unlike linear regression, this model captures a realistic feature of our biological hypothesis that discharge affects recruitment in high-discharge years but does not substantially affect differences in recruitment among low- to medium-discharge years.

In a separate, exploratory analysis, we compared models of every possible combination of the 11 environmental variables in Table 2, with or without S . Interaction terms were not included. All variables were modeled as simple linear effects, except that median discharge over the summer growing season was modeled with a threshold effect using the threshold selected for the discharge model. Some variables were considered in each of three periods of interest: (i) the summer growing season; (ii) the “critical emergence period” from 15 May to 15 June when newly emerged fry might be most sensitive; and (iii) “spawning and incubation period”, defined a priori to span the prewinter portion of incubation

time from 20 July (the earliest date spawning is typically observed) to 25 October (the latest date water temperature differed appreciably from midwinter levels during 2007–2011 when actual water temperature observations replaced the modeled temperatures used elsewhere). Temperature was expressed as total degree-days in °C over the period of interest. We used the Richards–Baker Flashiness Index (Baker et al. 2004) to represent the variation in discharge within each period. Although flashiness is typically used to compare the hydrology of different streams over a multi-year time scale, we chose it as a potentially useful descriptor of intra-annual variation in discharge because it incorporates both the frequency and magnitude of fluctuations in discharge into a single statistic.

Model fitting and assumptions

All models were fit using least squares linear regression on **log productivity (the natural logarithm of recruits per spawner)**. The regression assumption that residuals were normally distributed was met for all models presented here (Kolmogorov–Smirnov test, $p > 0.23$ indicating failure to reject the null hypothesis of normality at the 5% significance level). Homogeneity of variance was established by graphical examination of residuals. Residuals from the basic model were also checked for first-order temporal (i.e., 1-year lag) autocorrelation using the Durbin–Watson test (Durbin and Watson 1950). The Durbin–Watson D statistic for the Chena River residuals was 2.30, indicating the absence of significant autocorrelation (the null hypothesis that the data were not autocorrelated was not rejected at the 5% significance level). The Salcha River residuals showed minor, negative first-order autocorrelation ($D = 2.86$, marginally significant at the 5% level). Positive autocorrelation indicating streaks of good or bad years is commonly problematic for stock–recruitment models (Quinn and Deriso 1999); however, minor negative autocorrelation is less troubling. It may be spurious or a weak sign of some alternating-year biological process, but it should not influence our limited inferences from the Salcha River models.

Model selection and evaluation

We used the information-theoretic approach (Burnham and Anderson 2002) to evaluate the performance of models and importance of variables. These analyses are based on Akaike’s information criterion adjusted for finite sample sizes (AIC_c), which reflects on whether the inclusion of extra parameters in a model improves the model’s likelihood sufficiently to justify the extra parameters. AIC_c is interpreted not according to its literal value, but by comparing it among alternative models of the same data; a difference in AIC_c (denoted ΔAIC_c) of two or more is convention-

Fig. 1. Basic Ricker model fit for the (a) Chena River (1986–2005) and (b) Salcha River (1987–2005). The dotted line indicates replacement — one recruit per spawner.

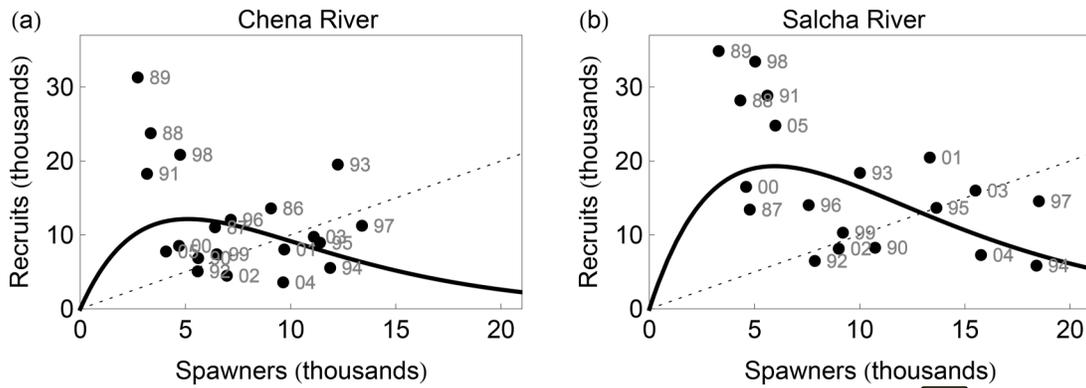
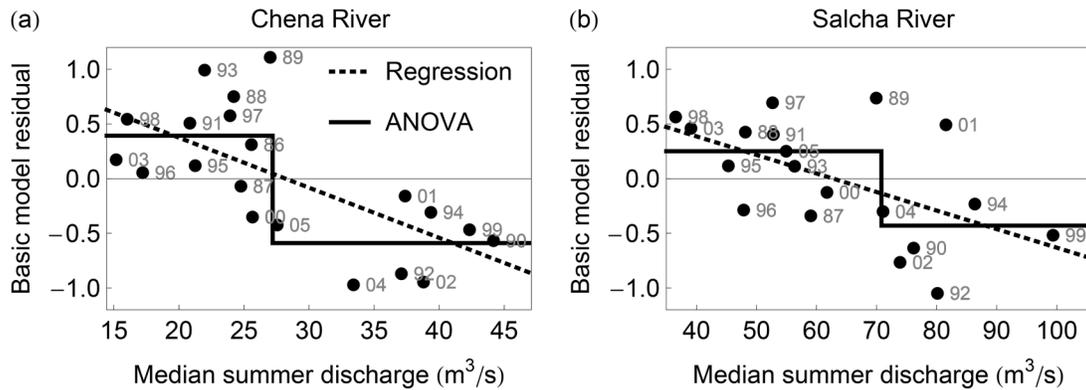


Fig. 2. Relationship between discharge during the summer growing season and Chinook salmon **log productivity** relative to the predictions of the basic Ricker model for (a) the Chena River and (b) the Salcha River. The dotted line shows the fit from linear regression, and the solid line shows the fit from an ANOVA model treating discharge as a categorical variable classified as either above or below 27.2 m³·s⁻¹ (for the Chena River) or 70.8 m³·s⁻¹ (for the Salcha River).



ally interpreted to indicate that the model with the lower AIC_c better balances explanatory power against the possibility of spurious parameters. The Akaike weight, calculated from AIC_c , reflects the relative weight of evidence in the data for each model in a set of candidate models. The relative importance of individual variables is expressed by adding the Akaike weights of all the models containing each variable (provided each variable appears in the same number of models, which was the case in our exploratory analysis).

The basic and discharge models were selected for detailed reporting for qualitative reasons: the basic model because it is widely used for management and the discharge model for evaluation of the a priori hypothesis that high discharge reduces recruitment. The full model was selected as the “best” model for the Chena River data, based on several criteria described later, including the fact that it had the lowest AIC_c in the exploratory analysis. To estimate the explanatory power of the models we selected, we used the coefficient of determination adjusted for the number of parameters, denoted R^2_{adj} , which reflects the proportion of variation in log productivity that could be explained by the model (standard R^2), adjusted downward to account for the expected reduction in variability with the addition of any parameter, even uninformative ones.

Explanation of the population decline

To determine whether the effects we detected could potentially explain the decline in Chinook salmon productivity, we plotted log productivity versus time and compared against the residual log productivity versus time from the basic Ricker model, the discharge

model, and the full model. If the visible decline in log productivity was reduced in a model’s residuals, we cautiously inferred that the model provides one plausible explanation for part of the decline.

Sensitivity analysis

We graphically examined the model’s sensitivity to our choice of discharge statistics. To determine whether the whole-season discharge effect we observed might be a signature of a stronger effect during a specific critical time period or a spurious artifact of the period we selected, we plotted the likelihood of the discharge model for all possible time periods ranging from 7 days in duration to the entire open-water season. We also examined the effects of using a different discharge statistic (e.g., some other quantile of discharge instead of the median or the number of days with discharge below a given threshold) to evaluate the sensitivity of the discharge effect to our particular choice of summary statistic. Our 20-year data set was too small to treat these values as model parameters without risk of overfitting, but the patterns evident in the post hoc graphical analysis are helpful for interpreting the model results.

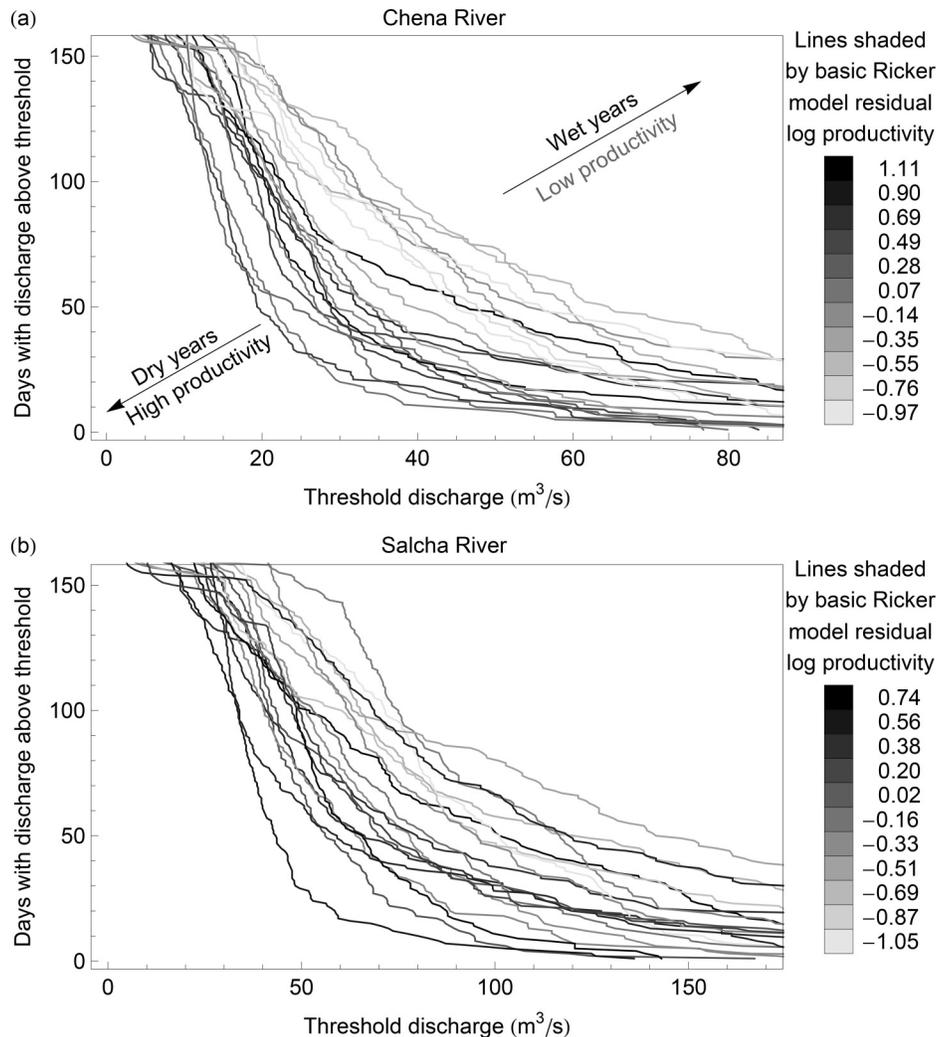
Results

Basic model and its residuals

The basic Ricker model explained a substantial portion of the variation in log productivity in the Chena River (Fig. 1a; $R^2_{adj} = 0.50$) and the Salcha River (Fig. 1b; $R^2_{adj} = 0.70$). The residuals from this model (the unexplained portion of log productivity) were inversely related to median discharge during the summer growing season in both the Chena River (Fig. 2a) and the Salcha River (Fig. 2b),

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Fig. 3. Annual (a) Chena River and (b) Salcha River discharge summaries shaded by residuals from the basic Ricker model (i.e., the portion of log productivity that is not explained by linear density dependence). Each line represents 1 year. Lighter-shaded lines indicate years of low productivity relative to the predictions of the basic model, and darker lines indicate higher than expected productivity. For each threshold discharge on the horizontal axis, the vertical position of a line indicates the number of days on which discharge exceeded the given threshold during the summer growing season. Therefore, lines toward the lower left corner of the graph represent low-discharge years.



meaning both rivers produced more recruits per spawner than the model predicted during low-discharge years and fewer recruits during high-discharge years. Compared with linear regression, this relationship was better described by an ANOVA model with a “threshold” effect of a categorical variable indicating whether median discharge did or did not exceed $27.2 \text{ m}^3 \cdot \text{s}^{-1}$ in the Chena River ($\Delta\text{AIC}_c = 6.4$) or $70.8 \text{ m}^3 \cdot \text{s}^{-1}$ in the Salcha River ($\Delta\text{AIC}_c = 1.2$).

The relationship between discharge and the basic Ricker model residuals was not limited to our arbitrarily chosen summary statistic, the median summer discharge. The large region of separation in Fig. 3a between high discharge – low productivity years and low discharge – high productivity years shows the discharge effect in the Chena River could be captured by many different summary statistics, including quantiles of discharge such as the median or threshold exceedance statistics (e.g., number of days with discharge greater than $25 \text{ m}^3 \cdot \text{s}^{-1}$). The discharge effect is similarly flexible in the Salcha River (Fig. 3b), except that one high-discharge year (2001) was anomalously productive.

Discharge model and its residuals

We compared four possible linear models containing spawner density (S), the categorical discharge effect (DISCH), or their inter-

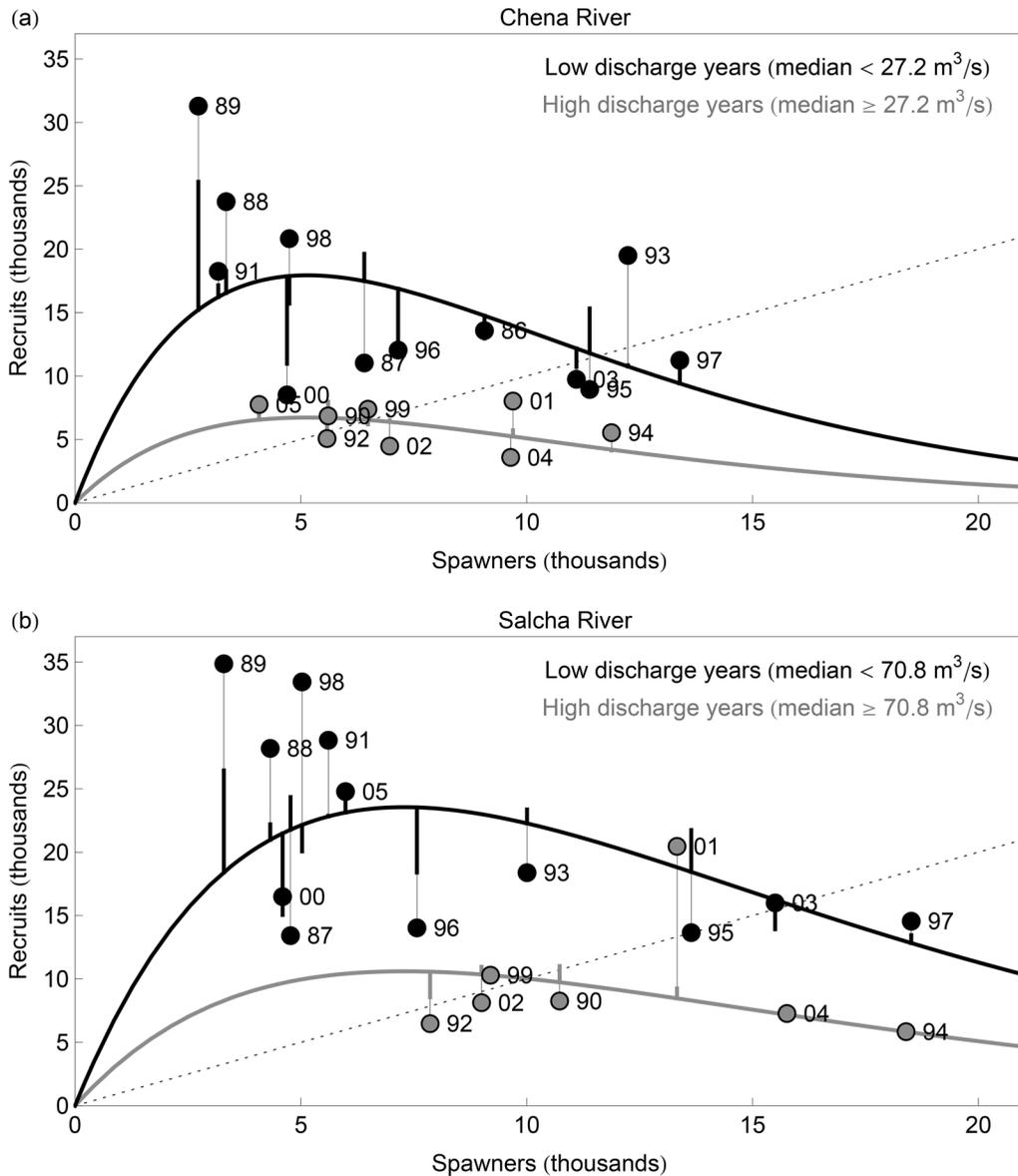
action, in a confirmatory analysis to evaluate the previously suspected relationship between discharge and recruitment (Table 3). The “discharge model”, containing main effects of the categorical discharge variable and spawner density, outperformed the basic Ricker model (which only included spawner density) in both the Chena River ($\Delta\text{AIC}_c = 13.83$) and Salcha River ($\Delta\text{AIC}_c = 6.52$). The improvement provided by this model is graphically apparent by comparing the main curves in Fig. 4 with the basic Ricker model in Fig. 1. This model also had more explanatory power for both the Chena River ($R_{\text{adj}}^2 = 0.79$ versus 0.50 for the basic model) and the Salcha River ($R_{\text{adj}}^2 = 0.82$ versus 0.70 for the basic model). An interaction term between discharge and spawner density did not improve the model for either river, which may imply that the effect of discharge arises by some mechanism other than discharge-dependent changes in density-dependent, intraspecific competition.

Variants of the discharge model for the Chena River, calculated using different time periods for median discharge, were used to graphically investigate the sensitivity of the discharge effect to the time period (Fig. 5). The large, darkly shaded area in the top left corner of the figure indicates that model performance was relatively strong across a broad range of potential time periods, beginning in late spring or early summer and ending in late sum-

Table 3. Model performance compared for all models in the confirmatory analysis of spawner density (*S*) and the threshold variable for median summer growing season discharge (DISCH).

River	Model	R^2_{adj}	ΔAIC_c	Weight
Chena	$-0.0001943 S - 0.98207 \text{ DISCH} + 1.2669$	0.789	0.00	0.837
	$-0.00016754 S - 1.2423 \text{ DISCH} + 0.00003478 S \times \text{DISCH} + 1.0664$	0.779	3.28	0.162
	$-0.00019515 S + 1.8624$	0.497	13.83	0.001
	$-0.98949 \text{ DISCH} - 0.18862$	0.222	24.18	0.000
Salcha	$-0.00013715 S - 0.79799 \text{ DISCH} + 1.3745$	0.823	0.00	0.688
	$-0.000091735 S - 1.4689 \text{ DISCH} + 0.00006049 S \times \text{DISCH} + 0.82776$	0.829	1.76	0.285
	$-0.000168 S + 2.1759$	0.696	6.52	0.026
	$-1.3196 \text{ DISCH} - 0.27667$	0.378	21.82	0.000

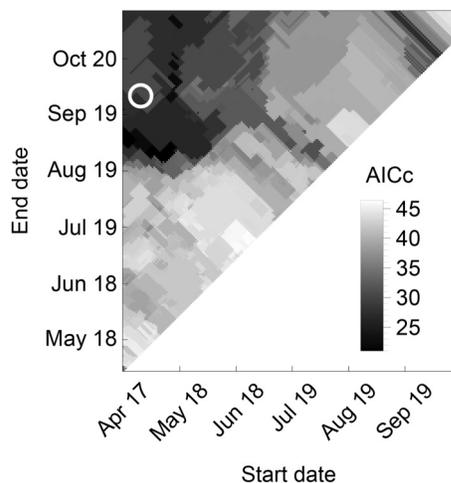
Fig. 4. Predictions of the discharge and full models for (a) the Chena River and (b) the Salcha River. The curves represent the predictions of the discharge model, and the thick vertical projections from each curve lead to the predictions of the full model, which incorporates temperature during spawning and incubation.



mer or early fall. The time period we chose a priori for the discharge model (23 April to 30 September) was located within this large region, but its AIC_c (29.7) was not the smallest in this set. The best models ($AIC_c = 21.0$) mostly used a range of dates beginning from late April to mid-May and ending from late August to early

September, visible as a large dark-colored streak in Fig. 5. This means that a model within those date ranges (e.g., 1 May to 31 August) would best represent the effect of discharge. We did not adjust the date range for our model accordingly, because this would effectively add two more parameters and risk overfitting; however,

Fig. 5. AIC_c values for the discharge model for the Chena River using different start and end dates for calculating median discharge. Lower AIC_c values (dark shading) correspond to better performance of the discharge model using the start and end dates specified by the axes. The center of the white circle corresponds to the time period selected a priori for the discharge model as used elsewhere in the paper, 23 April to 30 September, which had an AIC_c of 29.7.



future researchers analyzing other rivers in the region are encouraged to choose an a priori range of approximately 1 May to 31 August to determine a discharge effect.

Exploratory analysis of other environmental variables to select the full model

In addition to the variables included in the discharge model, we considered ten other environmental variables derived from discharge and temperature records (Table 2) in an exploratory analysis. The top models (ranked by ΔAIC_c relative to the model with the lowest AIC_c) from the set of all linear models of any of the 12 predictors are listed in Table 4. The two main predictors selected a priori for the discharge model, spawner density and the threshold effect of median discharge during the summer growing season, were by far the strongest supported in this broader analysis for both rivers; both appeared in nearly all models with substantial Akaike weights, so their total variable weights (Table 2) were very close to 1 (both >0.999 in the Chena River and >0.976 in the Salcha River).

Temperature (degree-days) during the 20 July – 25 October spawning and incubation period was the third-highest-weighted variable for the Chena River (0.797) and was also included, along with the two variables from the discharge model, in the model with the lowest AIC_c for the Chena River (Table 4). Comparison of this variable against the residuals from the Chena River discharge model (Fig. 6a) shows that its effect is driven by a much lower productivity than predicted in the 3 years with the lowest temperature during this period. Because of the biological plausibility of a negative temperature effect in the coldest years near the northern edge of the species' range, in combination with the relatively strong weight of this variable, we included it in the "full model" along with the variables from the discharge model. The full model was a modest improvement over the discharge model for the Chena River ($\Delta AIC_c = 4.93$; $R_{adj}^2 = 0.85$ versus 0.79 for the discharge model). Its predictions are shown as vertical projections from the curves that represent discharge model predictions in Fig. 4a.

The three next highest-ranked variables for the Chena River were too weakly supported for inclusion in the full model, but we plotted them against the residuals from the discharge model to identify trends that might be worth revisiting in future analyses. Productivity was lower than the discharge model predicted dur-

ing most years with a flood peaking above $200 \text{ m}^3\text{-s}^{-1}$ during the spawning and incubation period (variable weight 0.347; Fig. 6b). A slight positive effect of the maximum flood peak during the summer growing season (variable weight 0.327; Fig. 6c) seems biologically unrealistic and probably spurious. A slight negative effect of flashiness during the 15 May – 15 June critical emergence period (variable weight 0.266; Fig. 6d) is plausible, but it was not supported strongly enough to include in the full model.

The exploratory analysis focused on the Chena River and was repeated for the Salcha River for the purpose of partially confirming the effects detected on the Chena River. The selected full model also performed well on the Salcha River (see vertical projections in Fig. 4b), ranking fifth highest by AIC_c out of 4095 possible models. However, it was only a slight improvement over the discharge model ($\Delta AIC_c = 0.18$; $R_{adj}^2 = 0.85$ versus 0.82 for the discharge model). The three highest-ranked models for the Salcha River (Table 4) included a positive effect of the average duration of floods above seven times the median flow (variable weight 0.452); however, this weakly supported, biologically implausible effect was not present in the Chena River (variable weight only 0.111) and was probably spurious. The effect of temperature during spawning and incubation, included in the full model, ranked fourth highest in the Salcha River (0.316), consistent with our conclusion from the Chena River that it might be a real, minor effect. The next three highest-ranked exploratory variables from the Chena River (maximum flood peak during spawning and incubation, maximum flood peak during the summer growing season, and flashiness during the critical emergence period) ranked poorly for the Salcha River, corroborating our conclusion that they do not have substantial effects.

Explaining the decline in productivity

Log productivity declined sharply in the Chena River from 1986 to 2005 (Fig. 7a), and the slope of this decline was increasingly reduced in the residuals from the basic model (Fig. 7b), discharge model (Fig. 7c), and full model (Fig. 7d). A similarly sharp decline in the Salcha River (Fig. 7e) was absent from the residuals of the basic, discharge, and full models (Figs. 7f–7h). This suggests that the basic model based on density dependence alone was sufficient to explain the decline in the Salcha River, but incorporating the effect of discharge was necessary to explain the decline in the Chena River.

Discussion

Variation in Chinook salmon productivity in the Chena and Salcha rivers was explained primarily by negative density dependence (as represented in the basic Ricker model) and secondarily by a strong negative effect of high stream discharge during the juveniles' first summer in the river. Weaker evidence linked low productivity to cold water during the prewinter period of egg incubation. Combined, these factors provided plausible explanations for the recent declines in Chinook salmon productivity in the Chena and Salcha rivers. In this discussion, we reason that our detections are probably not spurious, but rather are ecologically credible through a variety of mechanisms that may be relevant to broader Chinook salmon declines.

Strength of evidence for the detected effects

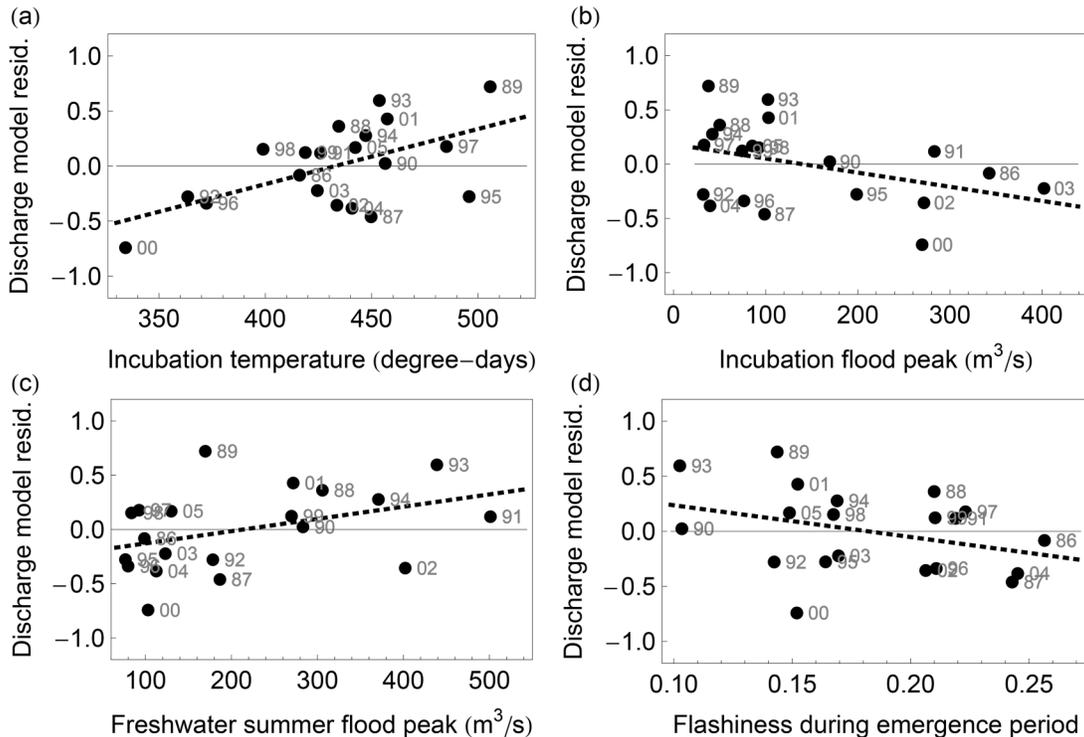
Analyses relating stock–recruitment data to environmental factors have been criticized in general because it is easy to mine data in an exploratory fashion, find some correlate that appears significant, and then imagine a post hoc mechanistic explanation for any such relationship (Hilborn and Walters 1992). Thus, many published environmental correlations with productivity have failed when retested with new years of data (Myers 1998). This criticism casts doubt not on the role of the environment in causing variability in productivity, but instead on the modeling practices used to detect such relationships. Myers (1998) prescribed

Table 4. Top ten models (ranked by ΔAIC_c relative to the best model) of log productivity of Chinook salmon in the Chena and Salcha rivers, from an exploratory analysis of all 4095 possible models for each river combining the variables in Table 2.

River	Model	R_{adj}^2	ΔAIC_c	Weight
Chena	$-0.00021648 S - 0.97806 DISCH + 0.0055618 INCTMP - 0.97251$	0.853	0.00	0.116
	$-0.00021125 S - 1.0368 DISCH + 0.005006 INCTMP + 0.00090902 SUMFLD - 1.0008$	0.865	1.16	0.065
	$-0.00021389 S - 1.0203 DISCH + 0.0053244 INCTMP - 2.5887 EMGFLSH - 0.44336$	0.865	1.19	0.064
	$-0.00020481 S - 1.1252 DISCH + 0.0040777 INCTMP - 0.0011996 INCFLD + 0.001091 SUMFLD - 0.57066$	0.883	1.72	0.049
	$-0.00021215 S - 1.0397 DISCH + 0.0049045 INCTMP - 0.00096502 INCFLD - 0.62198$	0.861	1.81	0.047
	$-0.00021858 S - 1.0633 DISCH + 0.0050252 INCTMP + 0.11997 FLDFRE - 0.85967$	0.857	2.34	0.036
	$-0.00018685 S - 1.173 DISCH - 0.0016164 INCFLD + 0.0013791 SUMFLD + 1.0284$	0.851	3.10	0.025
	$-0.00021852 S - 0.99185 DISCH + 0.0053411 INCTMP + 1.7741 SUMFLSH - 1.1845$	0.851	3.17	0.024
	$-0.00020941 S - 1.0693 DISCH + 0.0048452 INCTMP - 2.337 EMGFLSH + 0.00082151 SUMFLD - 0.52032$	0.874	3.24	0.023
	$-0.00020975 S - 1.079 DISCH + 0.0046935 INCTMP - 2.5243 EMGFLSH - 0.00093493 INCFLD - 0.11691$	0.872	3.47	0.020
Salcha	$-0.00013271 S - 0.9698 DISCH + 0.17829 FLDDUR + 1.0919$	0.853	0.00	0.070
	$-0.00013532 S - 1.0288 DISCH + 0.0074707 EMGTMP + 0.22698 FLDDUR - 0.51836$	0.872	0.40	0.057
	$-0.00014625 S - 0.88624 DISCH + 0.0034999 INCTMP + 0.15812 FLDDUR - 0.22801$	0.869	0.74	0.049
	$-0.00012842 S - 0.99431 DISCH + 0.0010197 SUMFLD + 0.76212$	0.846	0.87	0.045
	$-0.00015233 S - 0.72331 DISCH + 0.004076 INCTMP - 0.19991$	0.846	0.94	0.044
	$-0.00013715 S - 0.79799 DISCH + 1.3745$	0.823	1.12	0.040
	$-0.0001218 S - 1.0829 DISCH - 3.2602 EMGFLSH + 0.20038 FLDDUR + 1.4501$	0.863	1.69	0.030
	$-0.0001309 S - 0.87899 DISCH + 0.2403 FLDFRE + 1.1619$	0.837	2.03	0.025
	$-0.00014249 S - 0.89977 DISCH + 0.0033891 INCTMP + 0.00085113 SUMFLD - 0.44577$	0.860	2.09	0.025
	$-0.00012493 S - 1.1332 DISCH - 3.0742 EMGFLSH + 0.007178 EMGTMP + 0.24591 FLDDUR - 0.11748$	0.881	2.61	0.019

Note: Model coefficients are based on variables calculated from discharge values (in $m^3 \cdot s^{-1}$) and temperatures (in $^{\circ}C$).

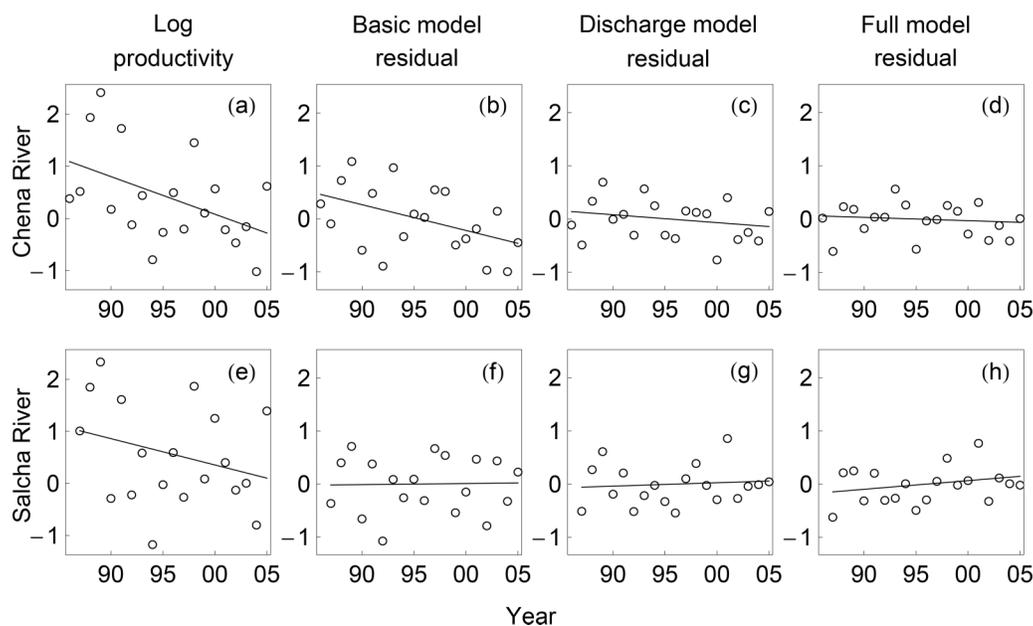
Fig. 6. Residuals from the discharge model plotted against the top four other environmental correlates identified in an exploratory analysis of the Chena River. During the prewinter spawning and incubation period, (a) cold temperatures and (b) large floods were possibly associated with poor recruitment relative to the discharge model's predictions. The next strongest relationships, with (c) a positive effect of maximum flood peak during the summer growing season and (d) a negative effect of flashiness during the critical emergence period, were weakly supported and probably spurious.



several guidelines for avoiding the methodological pitfalls that lead to spurious detections. We followed these when applicable, including (i) carefully separating confirmatory and exploratory analysis, (ii) honestly reporting the number of possible correlates investigated in exploratory analysis, (iii) correcting for — or in our case confirming the insignificance of — temporal autocorrelation, (iv) testing results in multiple systems, and (v) accounting for spawner abundance.

By these standards, our confirmatory analysis provides strong evidence that high discharge negatively affects Chinook salmon productivity in the Chena and Salcha rivers. The fact that a similarly strong effect can be observed across a broad range of discharge summary statistics (Fig. 3) and over a broad range of time periods (Fig. 5) suggests that the effect is not spurious. The Salcha River data are not completely independent of the Chena River data because environmental conditions and recruitment esti-

Fig. 7. Trends over time in log productivity (*a, e*) and residual log productivity left unexplained by the basic Ricker model (*b, f*), discharge model (*c, g*), and full model (*d, h*) for the Chena and Salcha rivers. The linear regression trend lines are intended to help visualize the direction of the data, not to imply that the real temporal trends are linear.



mates for these nearby rivers covary (see Methods), but the combined data still constitute stronger evidence than the Chena River data alone. It is encouraging that our model correctly predicts different population responses in the only year in which the qualitative discharge variable differed between the two rivers; the 2005 brood year experienced a high-discharge year in the Chena River with correspondingly low productivity and a low-discharge year in the Salcha River with correspondingly high productivity (Fig. 4).

We tentatively concluded that the variables we modeled — especially density dependence and discharge — explained the recent decline in Chinook salmon in the Chena River. Density dependence alone explained the smaller decline in the Salcha River's productivity, although the discharge effect was still useful for explaining other interannual variation in the Salcha River. Inferences about “explaining the decline” are drawn from the fact that the decline is present in log productivity, but not in residual log productivity from our full model. This is not conclusive evidence that we have a correct or complete explanation of the decline; instead, it means the data are consistent with the possibility of a causal relationship. This is the only group of variables so far identified as having appropriately large effects in the specific years necessary to explain the decline.

The marginally significant negative effect of cold water during the spawning and prewinter incubation period (Fig. 6a) was identified from exploratory analyses of the Chena River data that included nine other exploratory variables. This effect was also detectable, but weaker, in the Salcha River. Because large exploratory analyses are likely to identify some effects by coincidence, the evidence for this effect is not as strong as the model weights suggest. The effect also may not be well represented by a straight-line model, which might allow many moderate-to-warm years to mask the significance of an effect only important in the coldest years. The temperature effect is biologically very plausible because these rivers are near the northern edge of the range of Chinook salmon, and temperatures can decrease the rate of development of fish eggs and individual mass at hatching (From and Rasmussen 1991), so the coldest years might produce relatively weak or late-emerging fry. The weakly supported, possible negative effect of large floods during spawning and incubation (Fig. 6b)

might also have been masked by the majority of years without such floods, but it is worth considering because redd damage during floods (from scouring or siltation or both) is a primary cause of poor egg-to-fry survival in Chinook salmon (Healey 1991; Greene et al. 2005). Our main conclusion regarding the negative effects of both low temperature and large floods during spawning and incubation, given the inconclusive evidence but high plausibility, is that they are worthy of continued investigation when new data are available.

Possible mechanisms by which discharge might affect productivity

Although stock–recruitment analysis is correlative and does not conclusively demonstrate cause-and-effect relationships, the strong association we detected warrants serious consideration of the possibility that variation in discharge causes the associated variation in productivity. For purposes of discussion, let us assume the relationship is causal as we evaluate ideas about the nature of the relationship using post hoc pattern analyses of the present study, as well as other findings on the life history, behavior, and environment of Yukon drainage Chinook salmon.

In many anadromous salmonid populations, density-dependent mortality regulates the population during a critical period ranging from several days to several weeks after the yolk is absorbed and exogenous feeding begins (Elliott 1989). We cannot test for a critical period with regard to density dependence in the Chena River because no within-year survival estimates are available. However, during mechanistic studies on the Chena River from 2007 through 2010, we qualitatively observed that abundance peaked in June and declined rapidly for several weeks before stabilizing sometime in late July or August (J. Neuswanger, personal observation). This is consistent with a critical period for density-dependent mortality, which raises the question of whether the effect of discharge is also exerted during a specific critical period, such as the first weeks after emergence when the swimming ability of the fry is weakest and they might be more susceptible to floods. However, the AIC_c plot of our discharge model with different start and end dates (Fig. 5) provides evidence that the discharge effect is strongest when the median discharge is calculated over the entire summer, not a briefer critical period. If this infer-

ence is correct, it greatly constrains the mechanisms to which we might attribute the discharge effect.

Mechanistic hypotheses are further constrained by the lack of a significant interaction term between discharge and density dependence. In both rivers, the effect of discharge did not depend on population density, and (equivalently) the density dependence of productivity was similar in high- and low-discharge years. The absence of an interaction between these terms tentatively rules out some otherwise promising mechanistic explanations that relate stream discharge to the carrying capacity of the system, because a difference in carrying capacity between high- and low-discharge years should manifest itself as a substantial interaction term.

The most plausible explanations for the discharge effect probably involve the long-term effects of numerous, sustained, moderate to very high discharge periods on fish survival, not the short-term effects of catastrophic floods. The first argument to support this claim is that a threshold relationship described the discharge effect much better than a linear relationship, suggesting that it matters whether discharge is generally low or generally high, but not **how** low or **how** high it is. Second, variables pertaining to individual flood severity (including the maximum flood peak, flashiness, and frequency and duration of large floods) were not significant.

One plausible mechanism by which prolonged periods of high discharge could inhibit salmon survival is by increasing depth and turbidity, thereby reducing the amount of photosynthetically active radiation reaching the substrate. This causes a sharp decline in primary production in the Chena River at a discharge of about $1024 \text{ ft}^3 \cdot \text{s}^{-1}$ ($29 \text{ m}^3 \cdot \text{s}^{-1}$; Benson et al. 2013), close to the $960 \text{ ft}^3 \cdot \text{s}^{-1}$ ($27.2 \text{ m}^3 \cdot \text{s}^{-1}$) median discharge threshold that separated years of high and low salmon productivity. A prolonged reduction of primary production would reduce the system's carrying capacity for aquatic invertebrates. However, the timing of any food limitation bottlenecks for these aquatic insect populations is unknown, as is the time lag between a reduction in primary productivity and a reduction in invertebrate populations sufficient to affect the prey density encountered by drift-feeding Chinook salmon. Low primary production early in the summer might affect prey abundance throughout the season. However, the discharge effect we seek to explain is most likely a whole-summer effect, and it is unlikely that late-summer fluctuations in primary production would have enough time to influence drift-feeding fish before winter. Insect abundance is probably controlled at an earlier date, and Chena River Chinook salmon consume a large number of terrestrial insects late in the summer that might compensate for such reductions (Gutierrez 2011).

A prolonged decrease in primary production is just one threshold-exceeding process that may have triggered a decline in salmon productivity; another might be a shift in salmon behavior in response to the difficulty of foraging during high-discharge periods. Chinook salmon fry in the Chena River are primarily drift feeders, meaning they face upstream into the current from a stationary position and dart back and forth to intercept items of food (Jenkins 1969; Piccolo et al. 2014). Turbidity caused by extremely high discharge inhibits such visual feeding; however, Chinook fry in the Chena River feed mostly on items detected within 10 cm of their positions (Neuswanger et al. 2014), and the river becomes turbid enough to inhibit detection at that distance only briefly during floods. A more likely hindrance to foraging during sustained, moderately high discharge periods is an increased density of small particles of drifting debris that fish can mistake as prey. Such debris is common in the Chena River (and most other rivers) even during low-discharge periods when the water is very clear. During low-discharge periods on the Chena River, Chinook fry spent up to 25% of their overall foraging time pursuing debris items they eventually rejected (Neuswanger et al. 2014), which corresponds to a 25% decrease in energy intake rate. Drift net

samples in the Chena River and elsewhere show that the density of this debris greatly increases during high-discharge periods, possibly without a proportional increase in prey (M. Wipfli, personal observation). Therefore, debris could cause a population-wide, density-independent reduction in foraging success during high-discharge years. Another aspect of high discharge that can reduce drift-feeding success is increased water velocity (O'Brien and Showalter 1993; Grossman et al. 2002; Piccolo et al. 2008). Sufficiently large increases in discharge might cause widespread increases in water velocity, reducing the availability of safe habitat with optimal velocities for drift feeding along the margins of the stream. Probably as a consequence of these effects (turbidity, debris, velocity), prey mass consumed by Chinook fry in the Chena River in 2008 and 2009 was negatively correlated with discharge (Gutierrez 2011).

Although high discharge reduces foraging success, that reduction must also increase mortality if it is to explain the population-level association between discharge and productivity. This would obviously happen if fish with reduced foraging success die of starvation. However, at a water temperature typical of the Chena River (12°C), juvenile Chinook salmon slightly larger than those in the Chena (92.5 mm mean length) survived experimental starvation for up to 6 weeks with minimal loss of condition and no mortality (Snyder 1980), and smaller brown trout (*Salmo trutta*) have been shown to survive starvation for 3 weeks without adverse health effects (Sundström et al. 2013). It is possible that starvation occurs during a critical period for density-dependent mortality in the few weeks immediately following the transition of fry to exogenous feeding (Kennedy et al. 2008); however, starvation seems to be an unlikely explanation for the effect of discharge throughout the entire summer. High-discharge periods reduce foraging success, rather than eliminating it completely. Given the long survival times under experimental conditions of complete starvation, Chinook fry can probably avoid dying of starvation on reduced but positive rations for a very long time. Instead, it is more plausible that these fish, seeking long-term growth, would take more risks to seek better habitat and expose themselves to predation long before they succumb to starvation.

We do not know which predators might be responsible for juvenile salmon mortality in the Chena River or when that mortality would occur. The piscivorous ducks *Mergus merganser* (common merganser) and *Bucephala clangula* (common goldeneye) raise broods on the Chena River, and we have observed them targeting Chinook fry. If Chinook fry are a major part of the diet of these ducks, as seems likely, then the number of fry consumed by ducks should be largely determined by the initial population of ducks each summer and their energy needs, and it is unclear how their consumption of Chinook fry would be dramatically higher during high-discharge years. The difference between high- and low-discharge years would be more consistent with predation by a species that is normally supported at high densities by other foods, but can prey heavily on Chinook fry during high-discharge years. We speculate that Arctic grayling (*Thymallus arcticus*) might fill this role. Although grayling are the quintessential insectivorous drift-feeders (Hughes and Dill 1990), they can be piscivorous in certain situations (Stewart et al. 2007). We do not know of conclusive evidence for or against the hypothesis that grayling sometimes prey on Chinook fry in the Chena River. We have often observed adult grayling drift-feeding in close proximity to Chinook fry without acting aggressively. However, grayling are so abundant that even a small minority of individuals feeding on Chinook fry under very specific conditions might still inflict high mortality on the Chinook population.

Predation by grayling might occur during high-discharge periods if the Chinook fry, in search of better foraging conditions, migrate downstream in the main current of the river and temporarily become a part of the "drift" upon which grayling are already feeding. Chinook fry are capable of long-distance downstream

and upstream migrations, as evidenced by the Canadian-origin Chinook fry that leave their natal streams and colonize small tributaries of the Yukon far downstream in Alaska (Bradford et al. 2001; Daum and Flannery 2011). In years with sustained high discharge, Chinook fry in the Salcha River system have been found in small tributaries farther upstream and in greater numbers than in low- to medium-discharge years, and fewer fry were observed in the main river during high-discharge years (C. Stark, Bering Sea Fishermen's Association, personal communication). These Alaskan Chinook fry are not known to emigrate from their natal river system like their Canadian counterparts, but not enough sampling has been done to rule out the possibility that Alaskan Chinook fry make such movements under certain circumstances, such as during prolonged periods of high discharge. Chinook fry emigrating from the Chena or Salcha rivers would be susceptible to a wider range of predators, including northern pike (*Esox lucius*), burbot (*Lota lota*), and sheefish (i.e., inconnu, *Stenodus leucichthys*). These piscivores are present, though uncommon, in the lower Chena and Salcha rivers, and their off-channel sloughs, so extensive within-system movement of Chinook fry might increase predation risk to an unknown extent.

Based on all the constraints developed above, one hypothesis for the discharge effect emerges as the most consistent with available evidence. Frequent or prolonged periods of at least moderately high discharge reduce foraging success (particularly because of increased water velocity and debris density), which compels Chinook fry to migrate more extensively within their natal stream, or emigrate from it, thereby exposing themselves to predators they would not otherwise encounter very often (grayling within the stream, or burbot and northern pike if they emigrate) and creating a density-independent difference in predation mortality between low- and high-discharge years. This highly testable hypothesis is very tentative, because only weak evidence is available to exclude other plausible explanations, including starvation mortality and the effects of discharge on primary production and habitat carrying capacity. Nevertheless, given the vast number of possibilities, this relatively narrow hypothesis may prove useful as a starting point for future mechanistic research. Such work could investigate (i) direct negative impacts of high discharge on individual foraging and growth; (ii) movement within and emigration from the natal river system in response to changes in discharge, particularly with a contrast between low- and high-discharge years; and (iii) the timing, location, and proximate causes of mortality, considering both starvation and predation.

Implications for broader Yukon River and Alaska Chinook salmon populations

Our analysis offers positive direction to future research into the worrisome decline in Chinook salmon runs throughout the Yukon River drainage. In addition to the freshwater density dependence and habitat variables we examined, several other potential mechanisms for the decline have been investigated (summarized by Schindler et al. 2013), including (i) anthropogenic and natural changes in ocean conditions, such as the Pacific Decadal Oscillation; (ii) marine bycatch of salmon by the commercial groundfish fleet; (iii) poor escapement quality because of harvest methods that disproportionately target the largest spawners; and (iv) pathogens such as *Ichthyophonus*. Although none of these factors are fully understood, to our knowledge no other study has identified a mechanism by which any of them, alone or in combination, seems to convincingly explain the recent Chinook salmon decline. Our analysis shows that freshwater environmental variables, normally associated with uninformative interannual "noise" in productivity, have aligned — either coincidentally or as a consequence of climate change — in a way that could have caused the long-term pattern of reduced productivity in the Chena and Salcha rivers. Given the strength of our results, the likely transferability of flow- and density-related mechanisms to similar

streams throughout the Yukon drainage, and the marine evidence that variation in Canadian-origin Yukon Chinook recruitment is primarily attributable to either freshwater or very early marine processes (Murphy et al. 2013), it is plausible that the freshwater mechanisms we investigated have contributed substantially to the broader decline of Chinook salmon. However, the ubiquity of the decline throughout Alaska (ADF&G Chinook Salmon Research Team 2013) in streams with different freshwater conditions suggests that more universal mechanisms are also involved. We therefore agree with Schindler et al. (2013) that the regional decline probably has multiple causes, all of which warrant further research. However, this paper strengthens the evidence that freshwater conditions are an influential piece of the broader puzzle.

Better understanding the accuracy, generality, and specific mechanisms behind the effects we detected will require expanded data collection and research on both population-level and individual-level processes. Mechanistic understanding may prove most relevant for anticipating the impacts of global climate change, which in the Yukon drainage is expected to cause higher temperatures, higher annual (but not necessarily summer) stream discharge, a longer open-water season, and earlier spring runoff peaks (Arora and Boer 2001; Manabe et al. 2004; Aerts et al. 2006). It would be particularly valuable to test whether the observed effects of discharge occur generally throughout the Yukon drainage. The required spawning stream-specific run reconstructions with concurrent stream discharge measurements are only available for the Chena and Salcha rivers, but long-term monitoring of Chinook salmon recruitment is expanding to more spawning streams in the Yukon River drainage and others nearby (ADF&G Chinook Salmon Research Team 2013). It would be valuable to continue this expansion to other individual spawning streams and to record stream discharge data concurrent with all recruitment records. However, these long-term efforts take many years to generate informative data series. In the meantime, mechanistic studies relating competition, predation, and foraging behavior to individual fitness could improve confidence in our understanding of population trends. Our results contribute to an understanding that salmon productivity is tightly coupled with environmental factors subject to climate change, but the dominant mechanisms of these relationships, and therefore their ultimate consequences for salmon in a changing world, remain important unanswered questions.

In summary, poor Chinook salmon productivity in the Chena and Salcha rivers was strongly associated with high stream discharge during the summer they spent in fresh water as fry. Weaker evidence supported the observation that cold water during spawning and incubation also reduced productivity. The hypothesis that these factors combined have caused the recent decline in productivity is consistent with both the statistics evaluated here and recent work on ecological processes in the Chena River (Neuswanger et al. 2014; Benson et al. 2013; Gutierrez 2011). Although available data cannot conclusively establish a causal relationship in these rivers or elsewhere, our findings do bolster the plausibility of the hypothesis that freshwater habitat variables such as discharge have contributed substantially to the greater Yukon drainage or statewide declines of Chinook salmon.

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