

Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative

Project Final Product¹

AN ASSESSMENT OF KWETHLUK RIVER CHINOOK SALMON FRESHWATER PRODUCTION

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ABSTRACT

Recent declines in the productivity and abundance of Chinook Salmon stocks throughout the Arctic-Yukon-Kuskokwim (AYK) region have resulted in restrictions to commercial and subsistence fisheries. These restrictions have highlighted a need for greater clarity into the dynamics that regulate these populations. In this report, we evaluate the role that freshwater environmental and density dependent factors have on Chinook Salmon returns to the Kwethluk River. Our Analysis provides a comprehensive look at the currently available data for Kwethluk River Chinook Salmon. Our results are presented in three synergistic chapters: chapter one, abundance, migration timing, and production of Juvenile chinook Salmon, Kwethluk River, Alaska, 2015-2018; Chapter two, a run reconstruction and management reference points for Chinook Salmon in the Kwethluk River, Alaska, 1992-2017; and chapter three, chinook Salmon population-level responses to weather anomalies during spawning and Incubation, Kwethluk River, Alaska.

In chapter one, we discuss initial evidence for potential density and environmental regulation of freshwater production. To assess freshwater density effects, we characterized the relationship between smolt abundance and spawning escapements and compared the freshwater relationship to the pattern seen in adult recruitment. This allowed us to consider the relative importance of density on the freshwater phase of the life cycle. Although we had very few years to evaluate the freshwater relationship the contrasts between the spawning stock and smolt abundances were high and yielded a pattern of density dependence in freshwater production that parallels the relationship seen in total recruitment, suggesting that the capacity of Kwethluk River Chinook Salmon maybe meaningfully regulated by the freshwater life stage. In addition to the evidence for freshwater density regulation of the population capacity, brood year fall water temperature was well correlated with the variability seen in smolt production. As brood year fall temperatures increased the condition and production of migrating juvenile salmon decreased.

In chapter two, run reconstructions and a spawner-recruit relationship were used to validate current escapement objectives. We concluded that current escapement goals for Kwethluk River Chinook Salmon are sound and recommend no change in policy. Our age structured analysis illuminated historic harvest selectivity for the oldest age classes (age-6 and 7). Recent management strategies of time, area and net size restrictions have appeared to reverse this trend and again we recommend no change in policy.

In chapter three, we present additional and more compelling evidence for population-level responses to environmental variation during the fall of the brood year. Above average brood year fall air temperature and precipitation were shown to negatively affect adult recruitment, indicating that above optimal water temperatures and flooding during spawning and incubation are important factors driving the overall productivity of Chinook Salmon in the Kwethluk River.

Our Analysis provides evidence that both the capacity and productivity of Kwethluk River Chinook Salmon are heavily influenced by the freshwater life stage. While there are

apparent density effects, climatic controls are outweighing density regulators during many brood years. By explaining a sizeable amount of the variability in production with environmental variables, which are realized during a brood year, managers may be able to anticipate down turns in productivity before adults recruit. However, forecasting the effects of current or hypothesized changes in environmental variable can have mixed results for single stock models. We therefore recommend that a multi-stock models (meta-analyses) be developed for the Kuskokwim basin to produce more precise and accurate preseason forecasts.

Chapter 1

Abundance, Migration Timing, and Production of Juvenile Chinook Salmon, Kwethluk River, Alaska, 2015-2018.

ABSTRACT

In an effort to better understand the life stages that are influential in determining the population trends of Chinook Salmon *Oncorhynchus tshawytscha* in the Kwethluk River, Alaska. We used a rotary screw trap to monitor the migration of juveniles in 2015–2018. The migration of juvenile Chinook Salmon initiated at or just before breakup, peaked in May and abated by the end of June each year. Estimated stratified recapture probabilities ranged from 1.7 to 8.7% and averaged 3.3% among years. In general, catch rates were greatest during higher stream flows and correlated positively with stage height. The total yearly abundance of migrating juvenile Chinook Salmon were estimated to be 216,524 (CV 0.15), 332,195 (CV 0.10), 353,412 (CV 0.8), and 114,780 (CV 0.19) fish in 2015, 2016, 2017, and 2018, respectively. Although we had very few years to evaluate the relationship between the spawning stock and juvenile abundances, the contrasts between them were high and yielded a pattern of potential density regulation in freshwater production that parallels the relationship seen in adult recruitment. In addition to the evidence for freshwater capacity, brood year fall water temperatures were also well correlated with the variability seen in, freshwater production, suggesting that the dynamics of Kwethluk River Chinook Salmon maybe meaningfully regulated by a combination of density and environmental drivers in the freshwater life stage. This study successfully provided some of the first estimates of the abundance, migration timing, and freshwater production dynamics of Juvenile Chinook Salmon in western Alaska, information critical to understanding Chinook Salmon in this region.

INTRODUCTION

Many Arctic-Yukon-Kuskokwim (AYK) Region Chinook Salmon populations have experienced recent declines in productivity and abundance, resulting in substantial restrictions to subsistence fisheries (e.g. 3-S-WR-11-17 and 3-S-WR-01-18). These restrictions have emphasized a need for greater clarity into the dynamics that regulate these populations (AYK SSI, 2013; ADF&G Chinook Salmon Research Team, 2013). The separation of mortality into discrete components of the lifecycle may emphasize their relative importance for Chinook Salmon returns, thus, providing managers and stakeholders with pragmatic expectations and guidance when responding to declining Chinook Salmon stocks (Moussalli and Hilborn, 1986; Mobrand et al., 1997; Beamish and Sweeting, 2009).

The freshwater life stage is thought to contribute substantially to the overall population dynamics of Chinook stocks (Healey, 1991), yet information about freshwater juvenile Chinook

Salmon production in the AYK Region is limited (AYK SSI, 2013). The pairing of migrating juvenile Chinook Salmon abundance estimates with adult escapements allows for the characterization of freshwater production dynamics.

The Kwethluk River provides an ideal platform to conduct this type of work. Adult escapements increased from an all-time low to above average escapements from 2013-2016 (Miller et al., 2014, and 2015; Webber et al., 2016; and Harper et al., 2018), creating a high contrast in spawning escapement and a natural experiment to assess the effects of increased spawner abundance on freshwater production. In addition to the effects of interspecific competition, weather patterns can have significant effects on salmon and their habitats, and are associated with low productivity of some Western and Interior Alaskan Chinook Salmon populations (Neuswanger et al. 2015, Ohlberger et al. 2016, Cunningham et al. 2018). Assessing the effect of environmental variables from spawning to seaward migration may provide insight into whether recent declines are driven by freshwater or marine environmental conditions.

The project site is located below nearly all of the suitable spawning habitat for Chinook Salmon in the Kwethluk River (Head and Liller, 2017). Migrations of stream-type juvenile Chinook Salmon are typically characterized by three downstream displacements (1) just after emergence (Reimers 1971), (2) in the fall and early winter as fingerlings redistribute from summer to wintering habitats (Park 1969, Bjornn 1971) and (3) during early-spring as juvenile smolt and make their seaward migration (Burril et al., 2010). It is assumed that much of the exploited rearing area is above the study site because, major movements have not been observed prior to the smolting period. Burril et al. (2010) observed migration occurring primarily in the early spring and summer and pilot studies by the U.S. Fish and Wildlife Service (USFWS) found modest fall redistributions below the study site. In addition, the lower Kwethluk River consists of a deeper, muddy-bottom channel, turbid water conditions, and is relatively uncondusive to rearing (Malison et al., 2014). These observations indicate that spring seaward migrating juvenile Salmon abundances would provide a robust index of freshwater production.

Rotary-screw traps are a common capture technique and have been successfully used to estimate population size, migration timing, survival rates, and other characteristics of migrating juvenile salmonids and other fishes (e.g. Kennen et al. 1994; Thedinga et al. 1994; Roper and Scarnecchia 1999; Miller and Sadro 2003; Eskelin 2004; Downs et al. 2006; Feyrer et al. 2006; Venditti et al. 2006; Volkhardt et al. 2007; Sykes et al. 2009; and Anderson and Stillwater Sciences 2011). Estimates of smolt abundance coupled with estimates of adult salmon escapement, can be used to assess the capacities of freshwater habitats and effects of fishery and land-use management practices (Moussalli and Hilborn 1986; Solazzi et al., 2000). This information would greatly benefit the management of this important subsistence fishery while ensuring continued conservation of Kwethluk River Chinook Salmon.

STUDY AREA

The Kwethluk River is in the lower Kuskokwim River drainage and originates in the Kilbuck Mountains, flows northwest for approximately 222 river kilometers (rkm), and drains an area of about 3,367 km² (Alt 1977). The site location is near the transition from a braided actively meandering river channel with high habitat complexity to a lower gradient. The region is characterized by, a sub-arctic climate, average yearly precipitation is approximately 50 cm, with the majority falling between June and October, and temperatures generally range from summer highs near 15°C to average winter lows near -12°C (Alt 1977). Peak stream flows generally occur in April and May as snowmelt runoff, although rain events can cause large peaks in discharge throughout the ice free period (Harper et al., 2018). The rivers in this area are commonly ice-free in the slow current sections by early May and freeze up during late October.

METHODS

Fish capture.— A rotary-screw trap was used to capture migrating juvenile Chinook Salmon at the Kwethluk River weir site (N 60.51828, W 161.09245, NAD 83) approximately 84 rkm upstream of the Kuskokwim River and 42 km south of Kwethluk, Alaska. The trap consisted of a revolving 2.13 m diameter aluminum 2-mm-mesh cone on aluminum pontoons. When in operation, the cone was nearly half submerged offering an entrance area for fish of ~ 2.13 m². Stream flow caused the trap cone to rotate and fish passing through the cone were collected in a live well located at the downstream end of the trap. The trap was deployed in the spring of each year as soon as the river was free of ice cover and was operated until the seaward migration of juvenile Chinook Salmon subsided. Before each sampling period, if needed, the position of the trap was adjusted according to changes in flow to maximize captures. The trap was checked at least twice daily and up to every two hours when debris loads were high. When the trap was checked, all fish were identified to species, counted and immediately released, except when fish were held for marking and measurement. Abundance was assessed using mark-recapture techniques, and age and size composition were described by measuring a subsample of all captured fish. The target number of fish for marking and demographic description were selected for the desired precision levels using the methods described by Carlson et al. (1998) and Bromaghin (1993), respectively.

Mark-recapture protocols.— Using the single rotary-screw trap we marked, released and recaptured fish to estimate recapture probabilities and abundance. A sub-sample of up to 365 fish per day were retained for marking and measurement. Fish were anesthetized using a buffered stock solution of MS-222 at a concentration of 40 mg/L (Schoettger and Julin 1967) with a target induction time of one to three minutes (CBFWA 1999). Fish were monitored to identify when a loss of reflex was reached, at which time the tagging procedure took place. The first year (2015), fish were batch marked with period specific top and bottom lobe caudal fin clips, using surgical scissors cleaned with alcohol. Caudal fin clips were also taken and retained at random for genetic identification during 2017 ($n=147$) and 2018 ($n=107$). To meet the objectives of an accompanying ocean survival study, during the remaining years (2016-2018), fish were individually marked using passive integrated transponder (PIT) tags. Deployment of

PIT tags followed the procedures described in the Columbia Basin Fish and Wildlife Authority manual (CBFWA 1999). Each tagging candidate greater than 55 mm fork-length (FL) was marked with a Biomark® Model TX1411SST PIT-tag (12 mm long, 2.1 mm diameter, 134.2 kHz, full duplex) inserted into the fish body cavity anterior to the pectoral fin using a pre-loaded 12-gauge needle. The tag number was read and documented by scanning all tagged individuals with a hand held scanner (Destron Fearing Corp., St. Paul, Minnesota; FS2001). Regardless of marking method, all marked juvenile fish were measured for FL (mm) and weighed to the nearest 0.1 g. A Fulton condition factor (K) was calculated from the length and weight data using the methods and recommendations described by Petrusso and Hayes (2001). Scale samples were collected from a random subset of measured fish (every tenth individual), with a daily maximum goal of 10 fish. Scale “smears” were collected from the preferred area as described by Jearld (1983) and retained for future processing. Once sample size goals were obtained, marked fish were transferred from buckets to a live well near the release site and allowed to recover. Recovery time in the live well was typically 6 to 8 hours. All marked fish were released each evening, about 200 m upstream of the screw trap. Any tag loss or mortalities observed in the live well were noted prior to release of the marked fish. Scales were aged following the guidelines of Mosher (1968), and juvenile ages are reported based on the number of winters the fish spent in fresh water followed by a plus sign (e.g., age 1+).

Environmental data.— Each year, water-stage height (ft-tenths) and water temperature (°C) were monitored upon arrival at the trap site. Each day, water stage was recorded in the morning (08:00 hours) and again in the evening (20:00 hours) and averaged daily. Relative stage height was calculated as the average daily measurement divided by the sum of the annual values. We monitored water temperature every hour year-round using a HOBO pressure transducer data logger (Onset, Pocasset, Massachusetts, USA; www.onsetcomp.com). The temperature logger was located on the bottom at a fixed position approximately 1–2 m in depth.

Data Analysis.— The abundance of migrating juvenile Chinook Salmon was estimated in a Bayesian framework using a closed population estimator (Bird et al., 2014) modified to incorporate the apparent shape (log-normal) of migration timing (Adkinson and Su 2001). The utilization of the functional form of migration timing allows for the estimation of abundance during periods when direct observations were not possible (e.g. in the early spring before the trap was operational due to ice conditions). Our stratified mark-recapture design includes daily mark and recapture data that are combined into 7-day strata in which recapture probabilities were assumed to be analogous. For strata where recapture information was not available the closest available time step was used as a proxy. The temporally stratified recapture data were arranged in an m-array format (Kéry & Schaub 2012) and are summarized in Table 1.

In order to effectively estimate abundance from the stratified capture histories (y), we first estimated the rate of detection p . Because the population was considered to be closed, a fish’s susceptibility to capture (a) at time t was fixed at 1. The capture histories were modeled as multinomial random variables with the recapture parameter $\pi_t = \Pr(y_t = 1 | a_t, p_t)$ where $p_t = a_t p$ and the total number of releases m_t . Because fish can be recaptured only once in the

same strata that they were marked, and fish cannot be recaptured prior to their release, values above and below the main diagonal were set to zero. The posterior distribution for the recapture history is

$$y_t \sim \text{Multinomial}(p_t, m_t) \quad (1)$$

The (unknown) true population size at time t , N_t was modeled as a negative binomial random variable conditional on p_t and the number of unmarked individuals captured at each time step n_t . The posterior distribution truncated at the observed catch for the true population size is

$$N_t \sim \text{Negative Binomial}(p_t, n_t) T(n_t, \leq \infty) \quad (2)$$

Total annual juvenile abundance (N) was the sum of the annual stratified (N_t) estimates:

$$N = \sum_t N_t \quad (3)$$

Because ice conditions precluded direct observations during the beginning of the seaward migration, we used p_t from the closest available time step as a proxy, and estimated n_t during that period using the apparent shape (log-normal) of migration timing. The number of unmarked individuals captured at each time step was modeled as a random variable from a Poisson distribution of $\lambda_t > 0$ (λ_t),

$$n_t \sim \text{Poisson}(\lambda_t) \quad (4)$$

$$\lambda_t = h \left(\frac{(\ln(t) - \ln(\mu))}{w^2} \right) \quad (5)$$

Where: h is the maximum stratified catch, μ is the strata at peak catch, and w^2 is the variance of migration timing.

For the evaluation of juvenile production, productivity was defined as the number of migrating juveniles (recruits) produced from a brood year divided by the number of spawning adults (stock) that were present in the Kwethluk River to produce that brood. To provide freshwater production estimates that properly propagate the uncertainty in the number of migrating juvenile chinook Salmon that were produced from spawning adults, we divided the aforementioned estimated posterior distribution of migrating juvenile Chinook Salmon by the estimated posterior log-normal distribution of spawning adults estimated in chapter 2.

To quantify the functional relationship between brood year linked (y) migrating juvenile abundance R_y and spawning escapements S_y and derive biologic reference points we fit a linearized Ricker stock-recruitment model (Ricker 1954).

$$\ln\left(\frac{R_y}{S_y}\right) = \ln(\alpha) - \beta S_y + \varepsilon \quad (6)$$

where α is the productivity parameter, β is the capacity parameter, and ε is independent normally-distributed process error with standard deviation σ^R . Maximum sustained production of migrating juveniles (R_{max}) and the stock size leading to maximum production (S_{max}) were estimated from the parameters of the Ricker model as:

$$S_{max} = \frac{1}{\beta} \quad (7)$$

$$R_{max} = \frac{\alpha}{\beta e} \quad (8)$$

We calculated accumulated temperature units (ATUs; °C) from the mean annual spawning dates (Harper et al., 2018) until the spring of the first year of life as the sum of average daily temperatures. To visualize temperature effects on condition and productivity we fit a series of linear regressions to annual maximum fall (period from spawning to freeze up) ATUs, productivity ($\ln(R_y/S_y)$), spawning abundances (S), and median condition (K).

The abundance estimation, and stock juvenile recruitment models were analyzed using Bayesian methods with JAGS (Plummer 2003). JAGS was called from R (R Core Team 2018) using package R2jags (Su and Yajima 2015). For both models three parallel Markov chains, starting at random initial values in the range of parameter space, were run during 2,000,000 iterations and the initial convergence phase was excluded by dropping the first 500,000 iterations to ensure convergence. We used the Brooks-Gelman-Rubin criterion \hat{R} (Brooks and Gelman 1998) and diagnostic plots to assess the convergence of chains to a stationary distribution. We specified diffuse prior distributions for all target variables (Table 1). Model code for this analysis is found in appendices A and B.

Assumptions associated with our closed mark recapture experiment included: 1) the population is closed to deaths; 2) all fish have the same probability of capture; 3) each time step has a constant capture probability; 4) marks are not lost between release and recovery; 5) all marks are reported; 6) all marked fish released are either recaptured or pass by the downstream capture site; and 7) all fish are properly identified to species. To ensure that all assumptions were met we took the following steps: For assumption 1 we kept mortality from handling and marking at a minimum and when it did occur we censored them from the data. The selected release site ensured that most recaptures occurred within a day of marking making death from other causes unlikely. For assumption 2 we investigated size selectivity in capture by comparing lengths of marked and recaptured fish using a Kolmogorov-Smirnov two-sample test that compares the largest unsigned difference (D) to the critical value (Sokal and Rohlf 1981). To maximize mixing with the population prior to recapture we selected a release site several river bends upstream of the trap. For assumption 3 we ensured that release times were constant, recovery times were adequate, flow rates were similar within strata, and the

operation of the trap was as consistent as possible and only moved prior to the start of a new strata. For assumption 4, tag loss from the PIT tags was assessed using tagging scars, the partial caudal fin-clips were clearly visible and did not regenerate in the short time period between release and recovery. For assumption 5 a standardized procedure was implemented to ensure all captured fish were examined for marks and all marks were reported. Assumption 6, we only marked fish that were greater than 55 mm and expected to be age one or older. Because almost all Chinook Salmon in the Kwethluk River spend one year in freshwater (Webber et al. 2016) before their seaward migration, and marked fish were expected to be on their seaward migration and pass the trap shortly after their release (Roper and Scarnecchia 1999). To meet assumption 7 we confirmed species identification using a single nucleotide polymorphism genetic marker (SNP; Habicht et al. in review) from a sub-sample of tagged fish.

RESULTS

We operated a rotary-screw trap at the Kwethluk River weir site, during 2015 through 2018, to capture out migrating juvenile Chinook Salmon from breakup until capture rates became less than 1% of the yearly total. The migration of juvenile Chinook Salmon initiated at or just before breakup, peaked in May and abated by the end of June each year (Figure 1). Each year ice conditions prevented earlier start dates and juvenile Chinook Salmon were captured on the first day of trap operation, indicating that the trap was likely not operational during the entire emigration. Our model estimates that 8.6, 7.6, 0.8 and 0.9% of the migration occurred before the start of operations in 2015, 2016, 2017, and 2018, respectively.

A total of 25,296 juvenile migrating Chinook Salmon were captured during the course of this study, of which 19,947 were marked and 586 were recaptured (Appendix 3). From the stratified mark recapture data and the apparent shape of run timing, we estimated that the total yearly abundance of migrating juvenile Chinook Salmon was estimated to be 216,524 (CV 0.15), 332,195 (CV 0.10), 353,412 (CV 0.8), and 114,780 (CV 0.19) fish in 2015, 2016, 2017, and 2018, respectively (Figures 2 and 3).

Tagged migrating juvenile Chinook Salmon ranged in length (mm), weight (g) and condition (k), from 55 to 105 mm FL, 1.7 to 11.6 g and 0.6 to 1.98, respectively. The distributions of size and condition varied across years (Figure 4). Salmon less than 55mm never comprised more than 2% of the total catch. During all years, three ages were identified and nearly all were estimated to be one year old fish (>97% annually). Most migrating juvenile Chinook Salmon longer than 95 mm FL were age 2 and most fish less than 55 mm were age 0, although there was some overlap in the length composition by age.

Mark-recapture assumptions were considered valid, and mediated by the methods described above. Mortality of tagged fish was low overall, and was less than 1% of all marked Chinook Salmon held in the release site live well. These mortalities were subtracted from the marked total in their respective strata. The Kolmogorov-Smirnov two-sample test comparing length-frequency distributions of marked and recaptured fish indicated no difference at $\alpha = 0.05$ for any of the sample years (2015 $D = 0.17$, $P = 0.80$; 2016 $D = 0.13$, $P = 0.96$; 2017 $D = 0.20$, $P = 0.59$; and 2018 $D = 0.23$, $P = 0.39$; Figure 5) suggesting no size selectivity in capture

and proper mixing of marked fish. The screw trap position was adjusted frequently prior to the start of new strata to ensure the greatest possible trap efficiency, given changing water conditions. All other trap operations were consistent each day, including tagging procedures, recovery times and release timing. As a result, daily recapture rates were similar within strata but varied across strata. The estimated stratified recapture probabilities ranged from 1.7 to 8.7% and averaged 3.3% among years (Figures 2 and 3). Significant relationships were found between relative stage height and annual daily recapture rates (2015 $r^2 = 0.23$, $P < 0.001$; 2016 $r^2 = 0.15$, $P < 0.001$; 2017 $r^2 = 0.36$, $P < 0.001$; 2018 $r^2 = 0.40$, $P < 0.001$; Figure 6) and in general, captures were highest during higher stream flows. Stage height and water temperatures were variable in and amongst years, but generally increased from spring to mid-summer. All marked Chinook Salmon were recaptured within the strata that they were released and most were recaptured the following day after release. Species identifications were correct on average 94% of the time, as determined by genetic analysis, with misidentifications split evenly between Coho (*O. kisutch*) and Chinook Salmon.

From the reported spawning escapements of 5,849 (2016; CV 0.31), 8,139 (2015; CV 0), 3,315 (2014; CV 0.01), and 1,075 (2013; CV 0.06) (chapter 2), we estimate freshwater production at 201 (CV 0.18), 100 (CV 0.10), 43 (CV 0.8), and 18 (CV 0.37) fish per spawning adult in 2015, 2016, 2017, and 2018, respectively. The Ricker functional relationship between brood year linked migrating juvenile abundance and spawning escapements yielded a linear relationship. Productivity (α) was estimated at 248 migrating juveniles per spawner (95% CI: 99 – 1,184). The escapement leading to maximum juvenile production ($S_{max}; 1/\beta$) is estimated at 4,179 fish (95% CI: 1,790 – 7,473). Maximum sustained production (R_{max}) of migrating juveniles was estimated at 392,387 fish (95% CI: 179,485 – 955,213). Note that estimates are imprecise and derived from very limited data that likely does not completely capture the full range of dynamics of freshwater production in the Kwethluk River. Although these parameter estimates should be viewed with caution, the emergent pattern and biological reference points do represent the current freshwater production dynamics and all process and observation uncertainty.

Brood year linked ATUs produced a sigmoidal pattern and illustrated clear differences in annual fall temperature regimes (Figure 7). As maximum brood year fall temperatures increased the condition (Figure 8a) and production (Figure 8b) of migrating juvenile salmon decreased. Similarly, as parental spawning abundances increased the production (Figure 9a) and the condition (Figure 9b) of their progeny decreased.

In addition to Chinook Salmon, other species captured in the screw trap included Chum Salmon (*Oncorhynchus keta*), Pink Salmon (*O. gorbuscha*), Coho Salmon, Sockeye Salmon (*O. nerka*), Sculpin (*Cottus spp.*), Dolly Varden (*Salvelinus malma*), Rainbow Trout (*O. mykiss*), Arctic Grayling (*Thymallus arcticus*), Northern Pike (*Esox lucius*), Whitefish (*Coregonus spp.*), Alaska blackfish (*Dallia pectorallis*), Lamprey (*Lampetra spp.*), Stickleback (*Pungitius spp.*) and Burbot (*Lota lota*).

DISCUSSION

In this study, we were able to quantify abundance, characterize run timing, and describe a pattern of freshwater production for migrating juvenile chinook Salmon in the Kwethluk River from 2015–2018. Although the duration of ice cover and later than expected break-up dates inhibited the enumeration of the entire juvenile Chinook Salmon out-migration, our sampling and modeling approach provided a robust framework to estimate total abundance and migration timing. The emerging relationships between the spawning stock, fall temperatures and migrating juvenile abundances suggests an incorporation of density and environmental regulation in freshwater production. The pattern in freshwater productivity parallels the dynamics in adult recruitment (chapter 2), suggesting that the over-all dynamics of Kwethluk River Chinook Salmon may be meaningfully regulated by the freshwater life stage.

Fluctuations in discharge and break-up appeared to be the largest factors influencing the timing and rate of migration of juvenile Chinook Salmon on the Kwethluk River. Consistent with previous studies (Burril et al., 2010), migration rates increased during high water events, daily migration timing occurred during early morning, and peak annual migration occurred from mid-May through mid-June. Each year ice conditions prevented earlier start dates and juvenile Chinook Salmon were captured on the first day of trap operation, indicating that the trap was likely not operational during the entire emigration. Migration timing indicated that the magnitude of missed observations was substantial for some years. This dilemma informed our unique modeling approach which incorporated the apparent run timing shape into the model structure. This approach produced more accurate and complete estimates of migration timing and abundance.

Although we had limited information to evaluate the relationship between spawning stock abundance and migrating juvenile abundances the contrasts between them were high and yielded a pattern of potential density regulation. The estimates of capacity from the juvenile and adult recruitments (chapter 2) are statically analogues and suggest that the total capacity of Kwethluk River Chinook Salmon maybe meaningfully regulated by the freshwater life stage. The estimated freshwater productivity (α) of 248 juveniles per spawner and the estimated productivity at adult recruitment of 5.4 returns per spawner (chapter 2) implies an average ocean survival rate of 2%. This estimate is consistent with the species average of 1 to 2% reported by Bradford (1995). These results are also consistent with other Chinook Salmon populations in Western Alaska that have been shown to be regulated by the quality and quantity of juvenile freshwater habitats (Whited et al., 2012).

We also identified differing temperature regimes during the spawning and incubation period (Figure 7) that appear to relate to condition and productivity (figures 8 and 9). We recognize that our measurements of water column temperature taken at the study site may be different than interstitial water temperatures within spawning habitats, as a result of intra-gravel flow paths, geomorphic setting, or the presence of groundwater (Zimmerman and Finn 2012). However, the apparent link between elevated spawning and incubation period

temperatures (measured at the study site) and fish productivity and condition, suggest that the study site and spawning site temperatures maybe interrelated. Spawn timing, fry emergence, and smolting are largely driven by temperature (Quinn 2005). This asynchrony in timing caused by differing temperature regimes may be the origin of the observed increases in the observed mortality.

Chinook Salmon that are hatched and emerge precociously are smaller at hatching, as alevins and as fry (Heming 1982; Fuhrman et al., 2018). Precocious emergence has been linked to reduced swimming ability, decreased foraging ability, and increased predation (Weber-Scannell 1991). For salmonids the emergence period is selected to correspond with ideal temperatures (Skoglund et al., 2011; Beer and steel 2018) and has direct implications to condition (Fuhrman et al., 2017) and fitness (Einum and Fleming, 2000). No incubation or emergence studies have been conducted for the Kwethluk River stock, and local adaptations have been well documented (e.g. Beachum and Murray 1985, Beachum and Murray 1986; Burt et al., 2011; Geist et al., 2006; Steel et al., 2012; Fullerton et al., 2017; and Fuhrman et al., 2018). Nonetheless, variable brood year fall temperatures indicate a potential for a differential in developmental timing and associated effects. Years with what appears to be early hatching and emergence have a lower productivity than years with late hatching and emergence (figures 7, 8 and 9).

Increased freshwater temperatures have differential effects on growth, size at emergence is generally negatively affected by increased temperatures (Fuhrman et al., 2018), however, when fish start to actively feed as fry and fingerlings the trend in size is reversed and fish grow faster and larger at increased temperatures (Banks et al., 1971). Although fish size at smolting is expected to increase with warmer temperatures their body condition remains suppressed presumably due to the deficit accrued during incubation (Figure 4). Condition indices also provide information about relative abundance (Arismendi 2011), with a good condition indicating favorable food availability or a sparse abundance of fish, and a poor condition can indicate an overpopulation of fishes (Bennett 1970, Blackwell et al. 2000). The physiological and productivity costs of early life stage elevated temperatures and intraspecific competition are illustrated by their relationship to fish condition (Figures 7 and 8).

While there are apparent density effects, climatic controls can outweigh density regulators in unstable environments and may be a significant driver of the population dynamics. For example, high stream discharge during juvenile rearing and late river ice breakup in the year of smolt outmigration are associated with low productivity of some Western and Interior Alaskan Chinook Salmon populations (Neuswanger et al. 2015; Ohlberger et al. 2016; Cunningham et al. 2018). In fact, the environment has a stronger influence on recruitment than spawning biomass over the observed stock sizes for many stocks (Szuwalski et al. 2014). Environmental variables have even been shown to mimic compensation (Sakuramoto 2009), making the identification of the source of mortality (density dependent or independent) difficult to discern. Like all Chinook Salmon, the regenerative process of the Kwethluk populations is defined as a function of parental fecundity and both density dependent and independent survivorship (Quinn and Deriso 1999). However, because spawning abundance, fall temperatures, condition and productivity all co-vary, it is unclear which processes is

dominate. We recommend further investigation into environmental variables that may be related to changes in freshwater habitat resulting in variations in mortality (see chapter 3).

This project design and modeling approach proved effective for estimating migrating juvenile Chinook Salmon on the Kwethluk River. This study successfully provided some of the first estimates of the abundance, migration timing, and freshwater production dynamics of Juvenile Chinook Salmon in western Alaska, information critical to understanding the dynamics of Chinook Salmon in this region.

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Table 1. Prior distributions for model parameters for abundance (top) and productivity estimations (bottom).

Parameter	Description	Prior
h	Maximum stratified catch	$\text{dnorm}(.001,.001)T(0,)$
μ	The strata at peak catch	$\text{dnorm}(.001,.001)T(0,)$
w^2	The variance of migration timing	$\text{dnorm}(.001,.001)T(0,)$
p	Recapture probability	$\text{dunif}(0,1)$
$\ln(\alpha)$	$\ln(\text{productivity parameter})$	$\text{dnorm}(0,1.0E-2)T(0,15)$
β	Capacity parameter	$\text{dunif}(0,1)$
σ	Variance in juvenile recruitment	$\text{dunif}(0,100)$

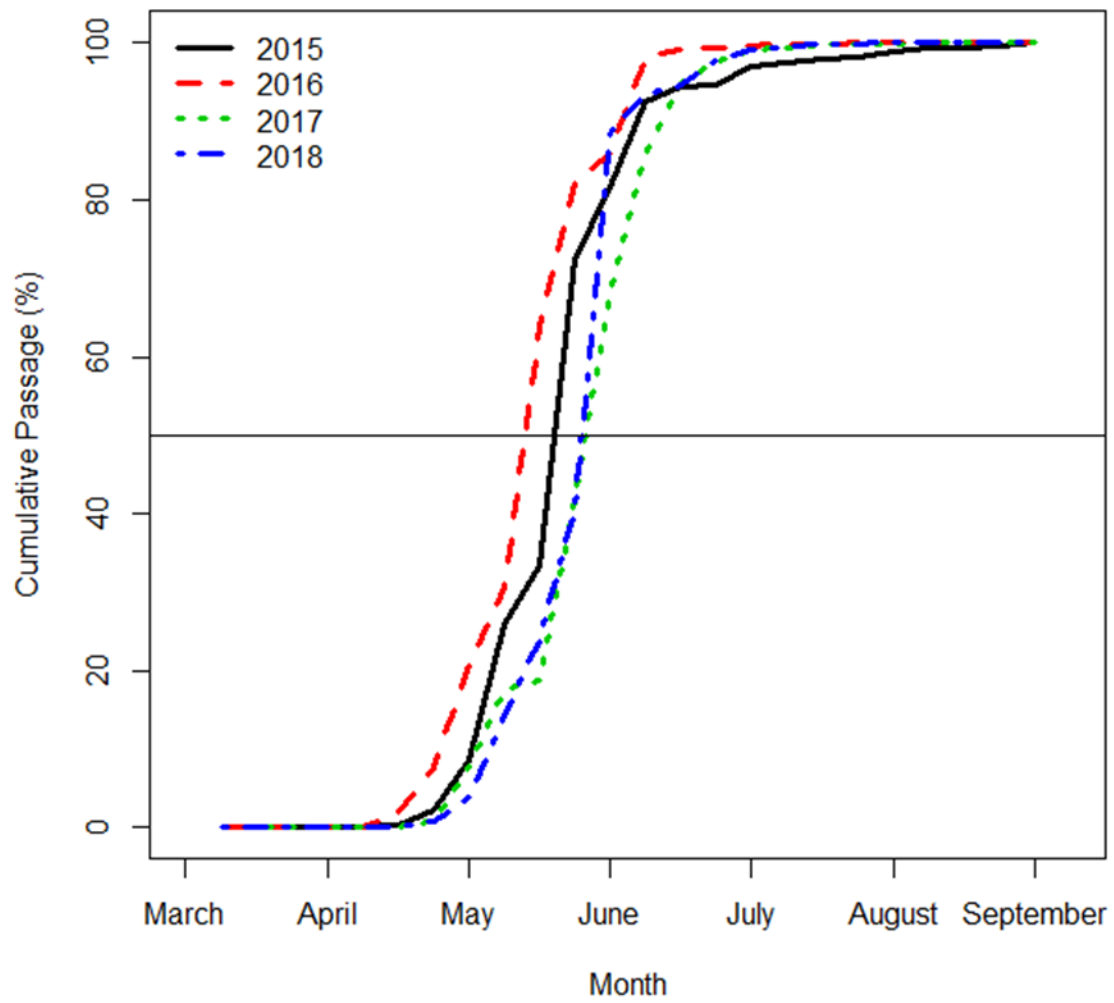


Figure 1. Estimated cumulative passage (%) of migrating juvenile Chinook Salmon at the Kwethluk River rotary-screw trap, 2015-2018.

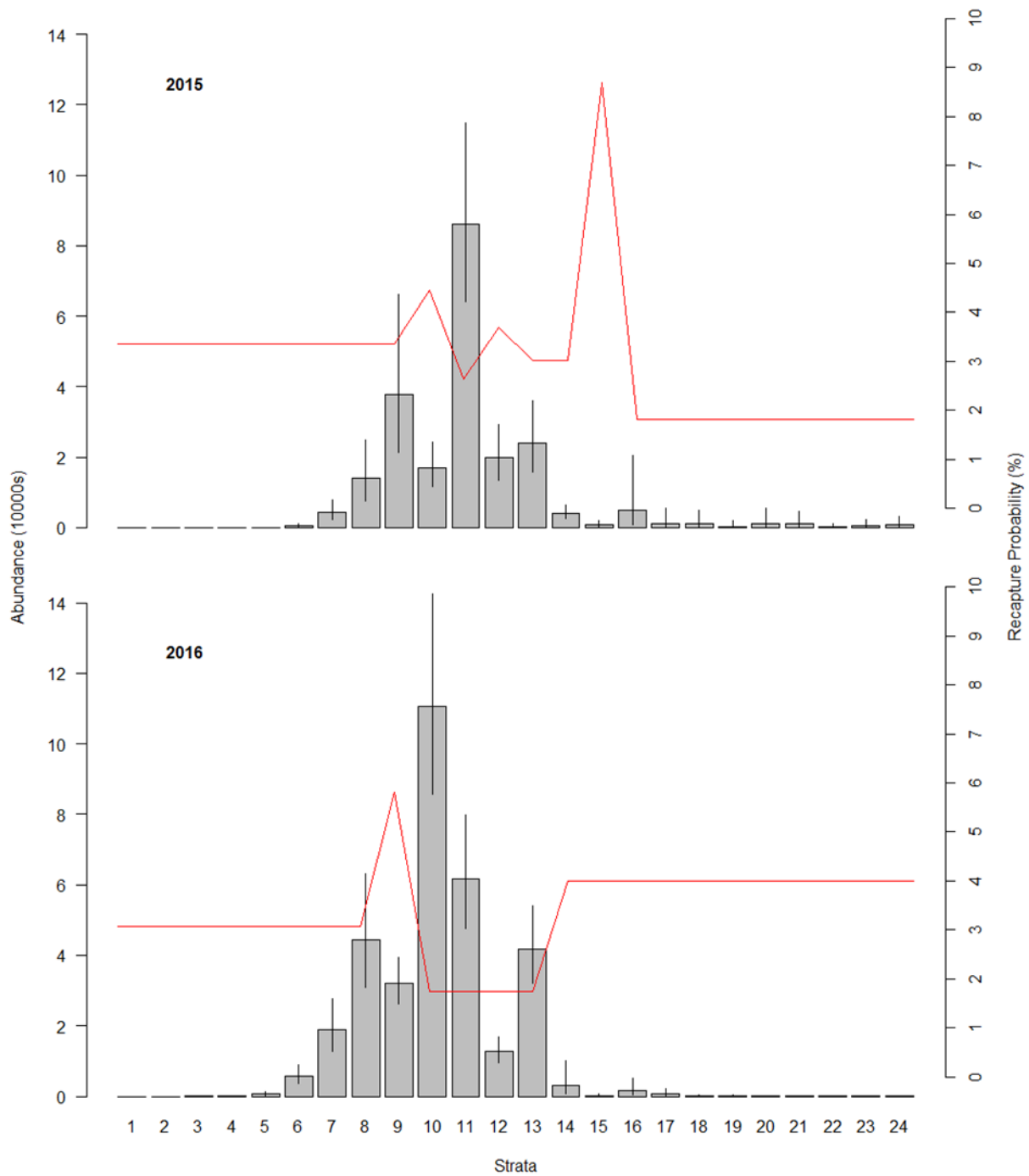


Figure 2. Migrating juvenile Chinook Salmon stratified abundance estimates (gray bars) and 95% credibility intervals, and estimated recapture probabilities (red line) at the Kwethluk River rotary-screw trap in 2015 and 2016. Strata are seven day periods starting on the first day of March to the last day in September.

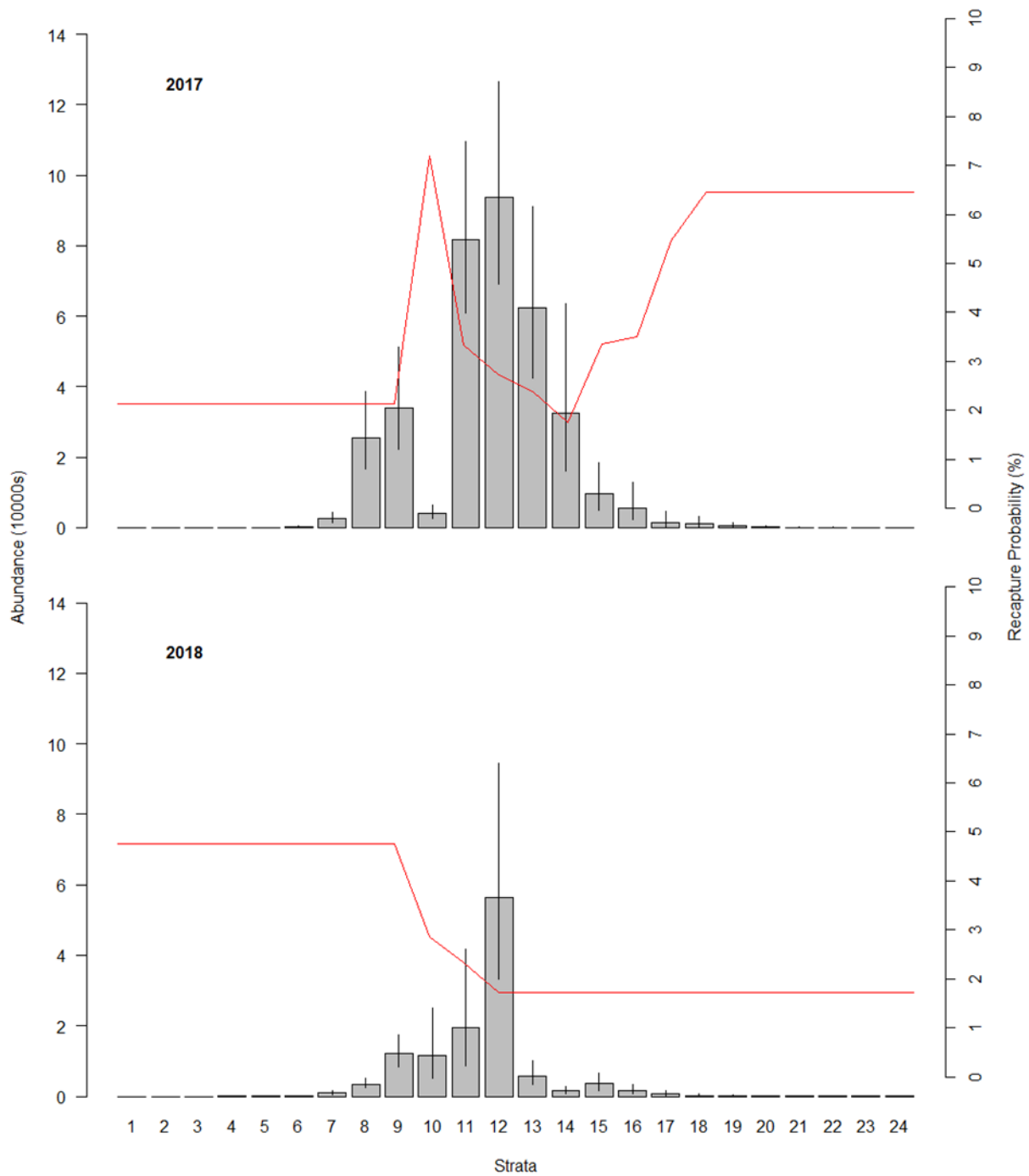


Figure 3. Migrating juvenile Chinook Salmon stratified abundance estimates (gray bars) and 95% credibility intervals, and estimated recapture probabilities (red line) at the Kwethluk River rotary-screw trap in 2017 and 2018. Strata are seven day periods starting on the first day of March to the last day in September.

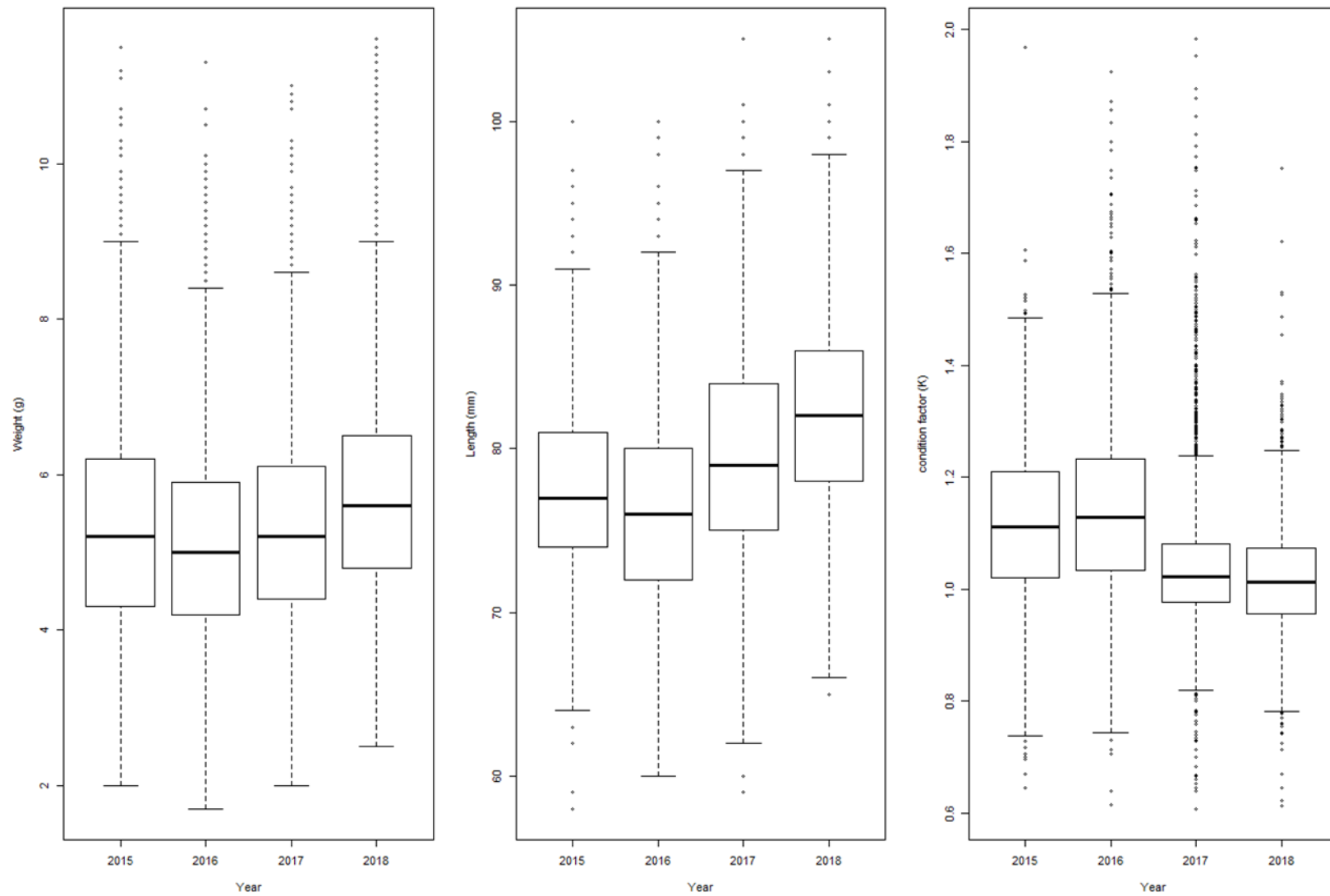


Figure 4. Total annual weight (g), length (mm) and condition (k) distributions for sampled Chinook Salmon at the Kwethluk River rotary-screw trap, 2015-2018.

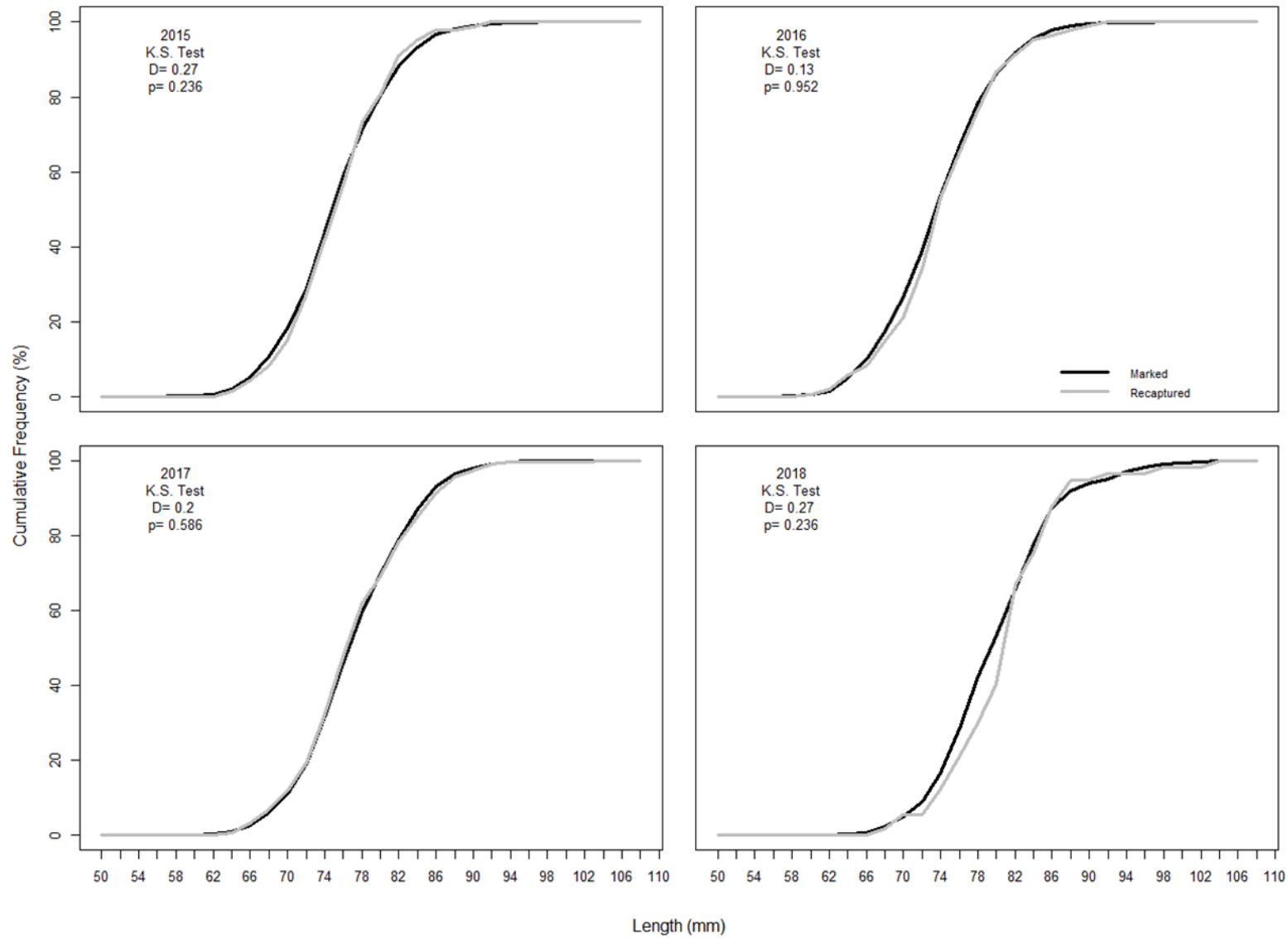


Figure 5. Cumulative frequency distribution Chinook Salmon marked and recaptured at the Kwethluk River rotary-screw trap, 2015-2018.

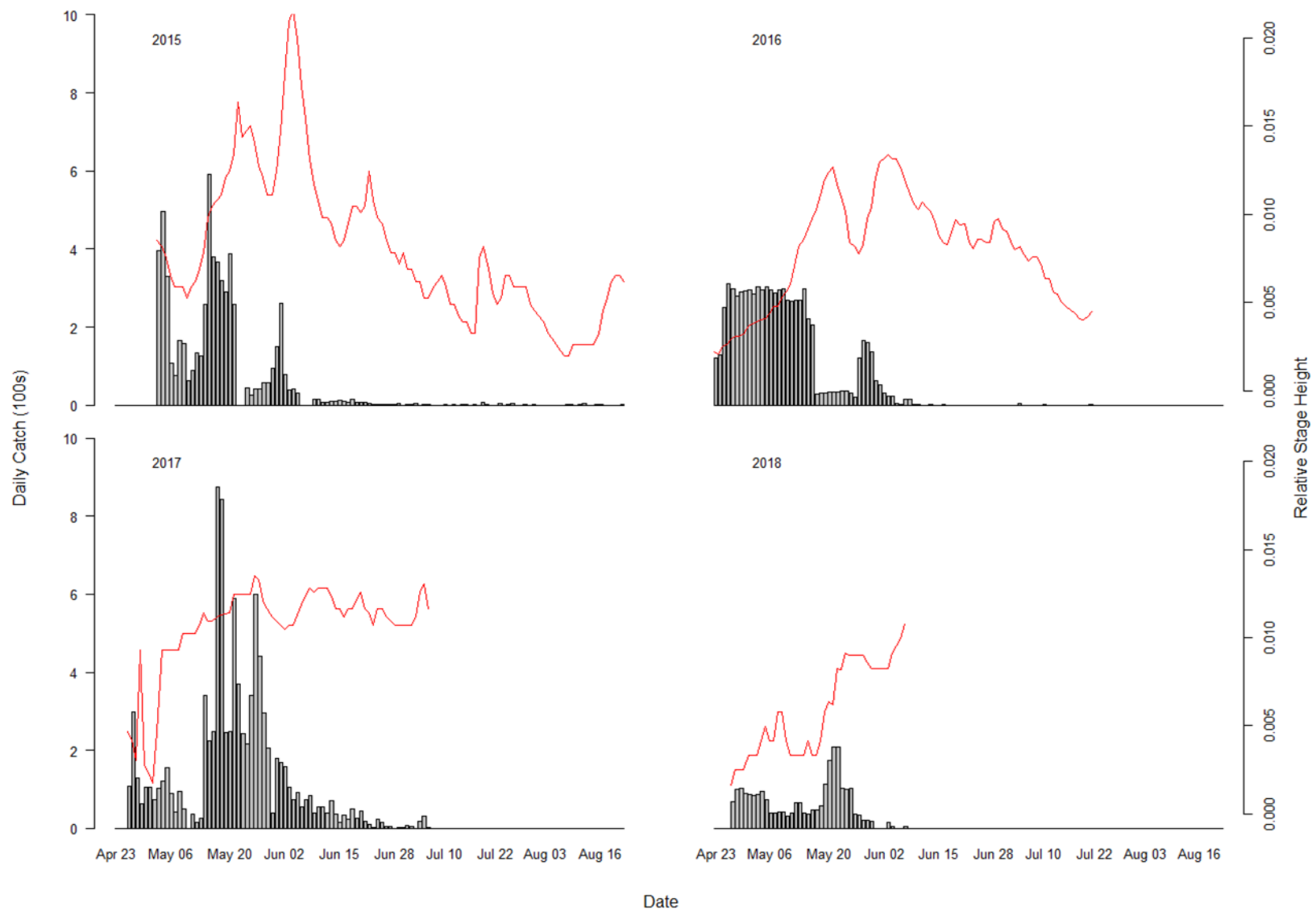


Figure 6. Total daily captures in relation to stage height for Chinook Salmon at the Kwethluk River rotary-screw trap, 2015-2018.

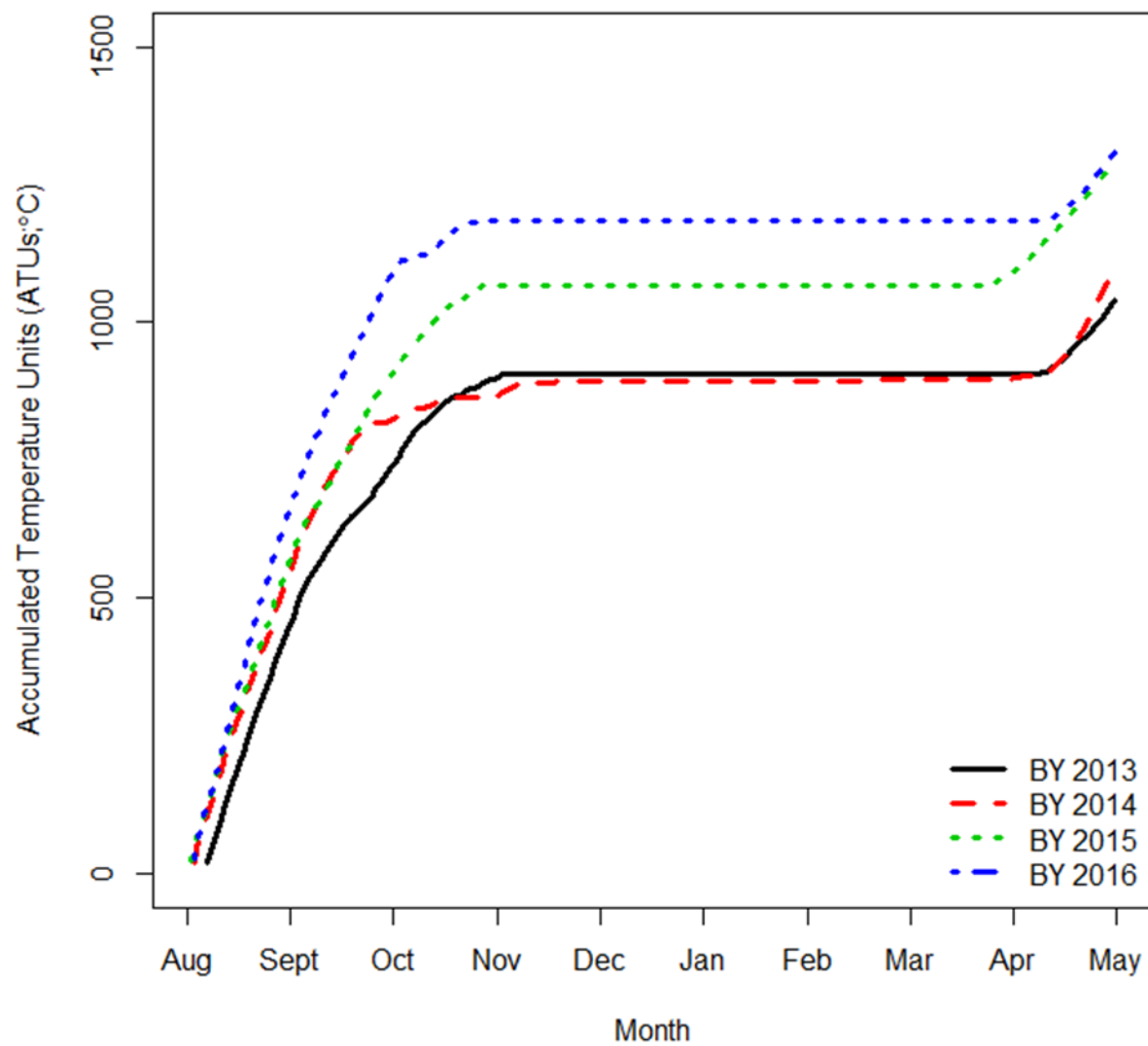


Figure 7. Accumulated temperature units (ATUs; °C) from the estimated median spawning date until May first for brood years 2013-2016 at the Kwethluk River rotary-screw trap.

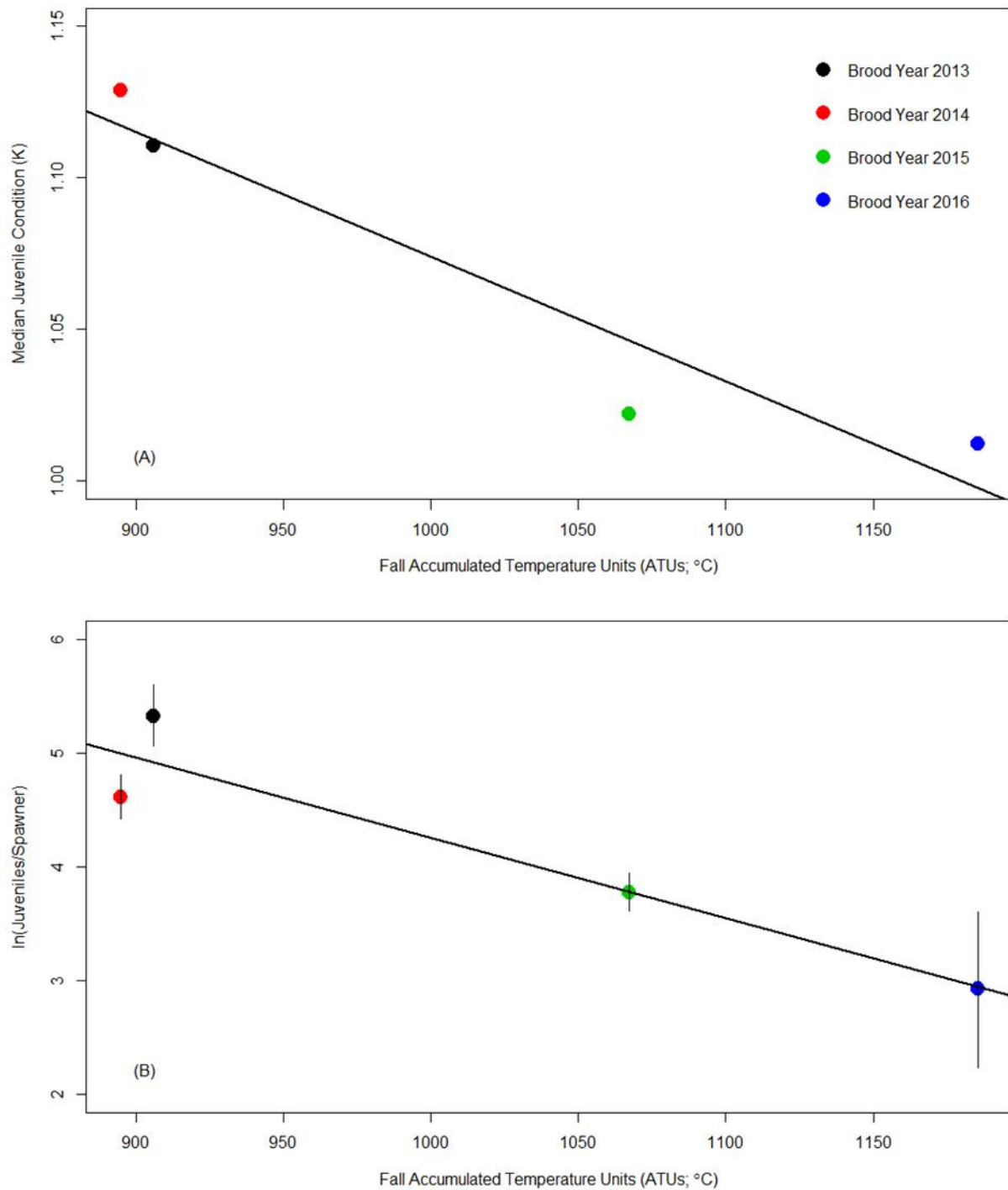


Figure 8. The relationship between brood year accumulated temperature units (ATUs; °C), median juvenile condition (K; A), Productivity (ln(juveniles/spawner); B) and 95% credibility intervals at the Kwethluk River rotary-screw trap, 2015-2018.

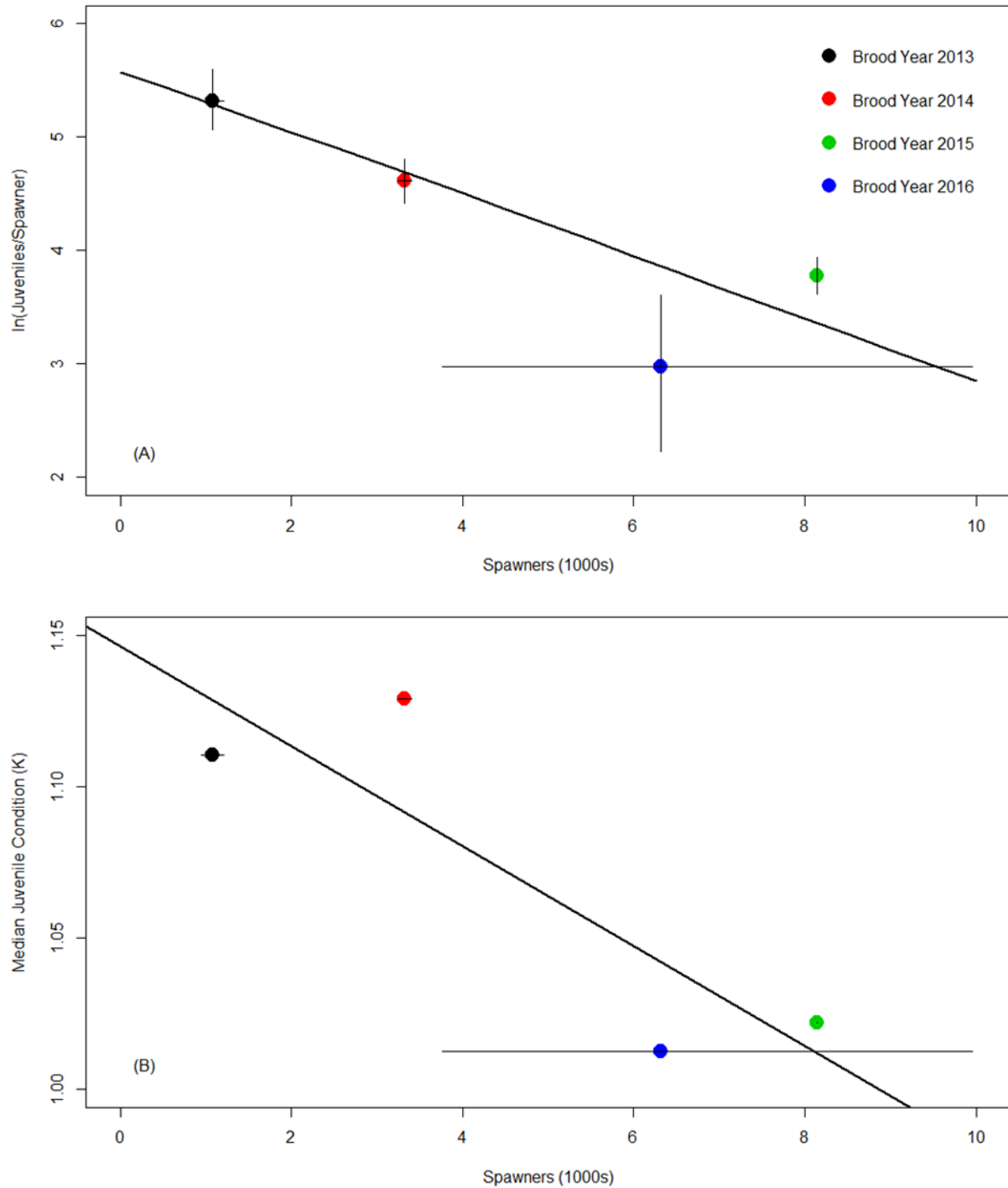


Figure 9. The relationship between adult spawning abundance, median juvenile condition (k; A), Productivity ($\ln(\text{juveniles/spawner})$; B) and 95% credibility intervals at the Kwethluk River rotary-screw trap, 2015-2018.

Appendix 1.—RJAGS model code for a closed population model to estimate Smolt abundance incorporating migration timing of Kewthluk River Chinook Salmon, 2015–2018.

```
" model{
  # Priors
  n_h ~ dnorm(.001,.001)T(0,)#maximum height
  n_w ~ dnorm(.001,.001)T(0,)#peak width (SD)
  n_mu ~ dnorm(.001,.001)T(0,)#strata at peak

  for (t in 1:(n.occasions-1)){
    obs_p[t] ~ dunif(0,1)#recapture probability
    #if recapture information is available allow p to vary with time
    #if not use next available value
    p[t]<-obs_p[r[t]]# r indexes available recapture data
  }
  # likelihood
  for (t in 1:(n.occasions-1)){
    marr[t,1:n.occasions] ~ dmulti(pr[t, ], rel[t])#m-array
  }
  # Define the cell probabilities of the m-array
  # Main diagonal
  for (t in 1:(n.occasions-1)){
    pr[t,t] <- p[t]# all fish were marked and recaptured in the same strata
  # Above main diagonal
    for (j in (t+1):(n.occasions-1)){
      pr[t,j] <- 0 # an individual can only be recaptured once in the same strata as it was marked
    } #j
  # Below main diagonal
    for (j in 1:(t-1)){
      pr[t,j] <- 0# an individual cannot be recaptured prior to its release
    } #j
  } #t
  # Last column: probability of non-recapture
  for (t in 1:(n.occasions-1)){
    pr[t,n.occasions] <- 1-sum(pr[t,1:(n.occasions-1)])
  } #t
  for (t in 1:(n.occasions-1)){
    N[t] ~ dnegbin(p[t],round(n[t]))T(round(n[t]),)# make distributions >= observed catch
    n[t] ~ dpois(lamda[t])
    lamda[t] <- n_h*exp(-0.5*pow(log(strata[t]/n_mu)/n_w,2))#log normal run time
  }
  #Smolt per spawner estimates
  #spawners are known
  spawner_sigma <- sqrt(log(pow(S_CV,2)+1))
  spawner_tau <- 1/pow(spawner_sigma,2)
  log_est_spawner <-log(est_S)
  spawner ~ dlnorm(log_est_spawner,spawner_tau)
  totalsmolt<-sum(N[])
  SmoltPerSpawner<-totalsmolt/spawner
}"
```

Appendix 2.— RJAGS model code for Ricker spawner recruit model of Kewthluk River juvenile Chinook Salmon, 2015–2018.

```
#####
# RICKER STOCK-RECRUITMENT #####
#####
"data{
  for(y in 1:Y) {
    smolt_sigma[y] <- sqrt(log(pow(smolt_CV[y],2)+1))
    smolt_tau[y] <- 1/pow(smolt_sigma[y],2)
    log_SmoltPerSpawner[y] <-log(SmoltPerSpawner[y])
    smolt[y] ~ dlnorm(log_SmoltPerSpawner[y],smolt_tau[y])
    Ln.Sm_Sp[y] <-log(smolt[y])
  }
}
model{
  # priors
  Ln.alpha ~ dunif(0,10)
  beta ~ dunif(0.0001,1)
  Smolt.tau ~ dgamma(0.0001,0.0001)
  # likelihood
  for(y in 1:Y) {
    S_sigma[y] <- sqrt(log(pow(S_CV[y],2)+1))
    S_tau[y] <- 1/pow(S_sigma[y],2)
    log_est_S[y] <-log(est_S[y])
    S[y] ~ dlnorm(log_est_S[y],S_tau[y])
    Ln.Sm_Sp[y] ~ dnorm(Ln.Sm_Sp.mu[y],Smolt.tau)
    Ln.Sm_Sp.mu[y] <- Ln.alpha-beta*S[y] # Ricker 1954
  }
  sigma.smolt <- 1/sqrt(Smolt.tau)
  alpha <- exp(Ln.alpha)
  S.max <- 1/beta
  R.max <- alpha/(beta*exp(1))
  for(y in 1:length(s2)) {
    pred.Ln.Sm_Sp[y] <- Ln.alpha-beta*s2[y]
  }
}"
```


Appendix 3. Summary of rotary-screw trap operation and capture on the Kwethluk River, 2015-2018. Strata are seven day periods starting the first day of March to the last day in September.

	Year	Strata																								Total
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
Mark	2015									386	719	1,817	731	704	124	67	45	12	11	4	12	10	2	5	7	4,656
	2016								1,044	1,754	1,903	940	202	575	62	3	0	0	4	3	1	0	0	0	0	6,491
	2017								420	704	304	1,409	1,614	1,176	511	297	169	53	60							6,717
	2018								112	560	243	298	752	92	26											2,083
Recapture	2015									12	31	47	26	23	1	5	1	0	0	0	0	0	0	0	0	146
	2016								31	101	53	6	0	3	2	0	0	0	0	0	0	0	0	0	0	196
	2017								3	20	21	46	43	27	8	9	5	2	3							187
	2018								0	31	6	6	14	0	0											57
Unmarked	2015									1,211	762	2,286	731	716	124	68	45	12	11	4	12	10	2	5	7	6,006
	2016								1,357	1,965	1,928	1,075	224	725	84	5	0	0	4	3	1	0	0	0	0	7,371
	2017								534	708	307	2,758	2,562	1,462	515	300	169	53	60							9,428
	2018								169	589	293	398	921	95	26											2,491

Chapter 2

A Run Reconstruction and Management Reference Points for Chinook Salmon in the Kwethluk River, Alaska, 1992-2017.

ABSTRACT

A Ricker spawner-recruit model was fit to estimates of escapement and recruitment, derived from relative and absolute abundance, harvest rates, and age compositions of Kwethluk River Chinook Salmon (*Oncorhynchus tshawytscha*) from 1992 to 2017. Bayesian statistical methods were employed to provide a realistic assessment of uncertainty in the presence of measurement error, serial correlation, and missing data. Estimates of escapement, harvest, run and return varied widely among years, ranging from 1,076 to 27,696; 378 to 8,525; 1,616 to 36,227; and 2,606 to 34,914 fish, respectively. From the run reconstruction and spawner-recruit relationship we estimate that on average an escapement of 5,022 (95% CI: 2,524–7,710) fish will result in maximum sustained yield, while maximum sustained recruitment is achieved with an average escapement of 7,934 (95% CI: 5,969–10,000) fish. Optimum yield and recruitment profiles were used to assess current escapement objectives and we conclude that current escapement levels for Kwethluk River Chinook Salmon (4,100 to 7,500 fish) are sound and we recommend no change in current policy. Our age structured analysis illuminated historic harvest selectivity for the oldest age classes (age-6 and 7). Recent management strategies of time, area and net size restrictions have appeared to reverse this trend and again we recommend no change in policy.

INTRODUCTION

The Kwethluk River, a lower Kuskokwim River tributary located on the Yukon Delta National Wildlife Refuge, provides important spawning and rearing habitat for Chinook Salmon (Alt 1977; U.S. Fish and Wildlife Service 1992). Adult Chinook Salmon returning to the Kwethluk River migrate 130 river kilometers (rkm) through the lower Kuskokwim River and another 90 to 160 rkm in the Kwethluk River before reaching their natal spawning grounds. These salmon pass through one of Alaska's largest Chinook Salmon fisheries (Fall et al. 2013), with up to 136,000 fish harvested annually (Smith and Liller, 2018).

Current management objectives set forth by the Kuskokwim River salmon management plan establishes a Sustainable Escapement Goal (SEG) of 4,100 – 7,500 Chinook Salmon for the Kwethluk River (Conitz et al. 2015). The SEG is a level of spawner abundance based on ranges of historic escapement that are thought to produce some level of sustained yield over a given period (Clark et al. 2014). The SEG methodology is typically implemented in situations where there is insufficient stock specific information to estimate biological reference points from a Stock Recruit Relationship (SRR) (5 AAC 39.222). The available 26 year time series of relative

and absolute escapement (Harper 1998; Harper and Watry 2001; Roettiger et al. 2002-2005; Miller et al. 2007-2009, 2015; Miller and Harper 2010, 2011a, 2012a, 2013a, 2014; Webber et al. 2016; Harper et al. 2018a and 2018b) and harvest (Smith and Liller, 2018) information spans multiple generations, captures the dynamics of the population under varied conditions, and is likely sufficient to characterize a meaningful SRR.

For Alaskan Chinook Salmon stocks where SRRs can be developed, management reference points have conventionally been derived from a Ricker SRR (ADF&G Chinook Salmon Research Team, 2013; Conitz et al. 2015). Typically age structured estimates of annual spawner abundance and harvest are combined to reconstruct the run (Shotwell and Adkison 2004). Run estimates are formatted into a brood table to obtain brood year recruits based on the year and age at which the fish returned (Clark et al. 2009; Bue et al. 2012). These estimates are then passed to a spawner-recruit analysis to estimate productivity, carrying capacity and derive reference points (Clark et al. 2009). A Ricker parameter estimation using a Bayesian framework allows for an accounting of the uncertainty in both the assessment data and the spawner-recruit relationship, resulting in a robust and realistic characterization of uncertainty (Rivot et al. 2004; Su and Peterman 2012; Fleischman et al. 2013) and less biased estimates of population parameters and reference points (Su and Peterman 2012).

In this paper, we employ a Bayesian statistical framework to estimate harvest policy parameters for the Kwethluk River Chinook Salmon stock. Our sequential two-step analysis includes (1) a run reconstruction that estimates historic escapement, harvest, and age structure information; and (2) a stock-recruitment dynamics component that is fit using a Bayesian framework to allow for simultaneous incorporation of both measurement error in the input information and process variation in the spawner-recruit relationship (Fleischman et al. 2013).

METHODS

Our analysis estimates run abundance and population dynamics parameters in two sequential models. The first model is a run reconstruction model, which, synthesizes age structured escapement and harvest estimations into recruitment estimates with uncertainty, expressed as a coefficient of variation (CV). The second model in our analysis is a Bayesian spawner-recruit model that assumes a Ricker SRR and time-varying productivity (Fleischman et al. 2013). This model treats run abundance estimates from the run reconstruction model as independently observed data with fixed uncertainty captured in the CVs. This observation error is incorporated into the spawner-recruit model by specifying the relationship of observable data to the estimates of the individual stock-recruitment quantities.

RUN RECONSTRUCTION

The stock specific observations required for annual run estimations and subsequent SRR are incomplete and require a variety of forecasting techniques to supply the missing information. We integrated estimates of Kwethluk River Chinook Salmon age structured escapement and harvest into our run reconstruction using a combination of direct observations at the Kwethluk River weir during 1992, 2000–2004, and 2006–2017 (Harper 1998; Harper and

Watry 2001; Roettiger et al. 2002-2005; Miller et al. 2007-2009, 2015; Miller and Harper 2010, 2011a, 2012a, 2013a, 2014; Webber et al. 2016; Harper et al. 2018a and 2018b), and Kuskokwim River mixed stock escapement, and harvest estimates (Smith and Liller, 2018; Liller personal communication).

Escapement

Abundance.– The counts for years with direct observations of Kwethluk River escapement are often incomplete due to flooding, holes in the weir, or problems with video operations; thus, to provide complete escapement estimations for years with incomplete data we used a hierarchical Bayesian estimation technique (Adkinson and Su 2001). The daily count (i) from year (y) and day (t) is a random variable from a normal distribution of mean (θ_{it}) and standard deviation (σ_t^2).

$$i_{y,t} \sim \text{Normal}(\theta_{y,t}, \sigma_t^2) \text{ and,} \quad (1)$$

$$\theta_{y,t} = a_y \left(\frac{(\ln(t) - \ln(\mu_y))^2}{b_y^2} \right) \quad (2)$$

Where: σ_t^2 is the variance of daily passage of day (t), a_y is the maximum daily passage of year (y), μ_y is the mean passage date for year (y), and b_y^2 is the variance of run timing for year (y). All upper hierarchical parameters were assumed to be a random sample from a normal distribution. Total yearly escapements S_y for years with direct observations are the sum of the observed and estimated daily counts ($i_{y,t}$).

For years in which there are no direct observations of escapement we used estimates derived from Kuskokwim River mixed stock escapement and scaling parameter estimates (Smith and Liller, 2018). Kwethluk River escapement can be proportionally related to the mixed stock escapement such that the expected number of fish counted in a year is:

$$S_y = \widehat{M}_y / \hat{k} \quad (3)$$

where \widehat{M}_y is the log-normally distributed total annual escapement of the mixed stock predicted by the model, \hat{k} is a normally distributed proportionality coefficient that scales the index to the mixed stock escapement, and S_y is the predicted count from the Kwethluk weir in year (y).

Age structure.– Age compositions of Chinook Salmon escaping to spawn in the Kwethluk River are modeled as an age conditional multinomial likelihood drawn from a common Dirichlet distribution. Formulating the shared Dirichlet distribution hierarchically allows age structure to fluctuate annually around a central tendency. The Dirichlet constructed from a series of independent Gamma distributions of can be expressed where

$$D = \sum_a \gamma_a \quad (4)$$

the concentration parameter (D) is the sum the expected age (a) frequencies (γ_a), which controls the variation in age structure between years, the age structure central tendencies:

$$\pi_a = \frac{\gamma_a}{D} \quad (5)$$

are proportions that sum to 1, and year-specific proportional age structures are drawn from the common distribution:

$$P_{y,a} = \frac{g_{y,a}}{\sum_a g_{y,a}} \quad (6)$$

$$g_{y,a} \sim \text{Gamma}(\gamma_a, 1.0) \quad (7)$$

Estimated escapement by age and year was the product of total escapement and the annual proportion of the age categories:

$$S_{y,a} = S_y * P_{y,a} \quad (8)$$

Total yearly estimated escapement is the sum of abundance at age across ages:

$$S_y = \sum_a S_{y,a} \quad (9)$$

Age samples ($x_{y,a}$) were collected annually and determined from scale analysis. Expected annual age proportions were informed using a multinomial likelihood:

$$x_{y,a} \sim \text{Multinomial}(q_{y,a}, n_y) \quad (10)$$

Where

$$q_{y,a} = \frac{S_{y,a}}{\sum_a S_{y,a}} \quad (11)$$

Annual sample sizes (n_y) specify the quality of age proportion information influencing how well the model fits the observed age samples.

Harvest

Abundance.—To estimate annual harvests of Kwethluk Chinook Salmon we assumed that there was not selective harvest among stocks. The annual (y) exploitation (U) rate estimated from the mixed stock run reconstruction (Smith and Liller, 2018) is a random variable from a uniform distribution, informed by a lognormal likelihood:

$$M_y \sim \text{logNormal}(\ln(\widehat{M}_y), \sigma^2), \quad (12)$$

where

$$\ln(\widehat{M}_y) = \ln(r_y(1 - U_y)) \text{ and} \quad (13)$$

σ^2 is the standard deviation of the estimated log normal mixed stock run reconstruction and r_y is the estimated mixed stock run following a lognormal distribution. The estimated annual Kwethluk River stock specific harvest was:

$$H_y = \frac{S_y}{(1 - U_y)} U_y \quad (14)$$

Age structure.– Commercial and subsistence mixed stock harvest age samples were obtained directly from ADF&G biologists and the age compositions of the harvest are modeled identically to the escapement age structure using equations 4 – 11. Age specific harvest was predicted by applying annual proportional age compositions ($P_{y,a}$) of the mixed stock harvest to the estimated total harvest for Kwethluk River bound Chinook Salmon:

$$H_{y,a} = H_y P_{y,a} \quad (15)$$

Run

Age structure.– The annual age specific in-river run ($N_{y,a}$) was the sum of age and year specific harvest ($H_{y,a}$) and escapement ($S_{y,a}$):

$$N_{y,a} = H_{y,a} + S_{y,a} \quad (16)$$

Abundance.–Total annual in-river run (N_y) was the sum of the annual age specific in-river run ($N_{y,a}$) estimates:

$$N_y = \sum_a N_{y,a} \quad (16)$$

Recruitment

The brood year (t) recruitment (R) from individual spawning events are calculated as the sum of annual age specific in-river run abundance indexed by brood year and staggered across multiple calendar years ($N_{a+y,a}$):

$$R_t = \sum_a N_{a+y,a} \quad (16)$$

STOCK-RECRUITMENT

Returns of Kwethluk River Chinook Salmon from the 1992 – 2010 brood years were modeled as a function of annual spawning escapement using a Ricker (1954) stock-recruitment model with an auto regressive (AR) lognormal process error (Fleischman et al. 2013). The base parameterization of the Ricker function is as follows:

$$\ln(R_y) = \ln(S_y) + \ln(\alpha) - \beta S_y + \phi\omega_{y-1} + \varepsilon_y \quad (17)$$

Where α is the productivity parameter, β is the (inverse) capacity parameter, φ is the AR lag-1 coefficient, ω_y is the model residual, and ε_y are the independent normally distributed process errors with standard deviation σ_R .

To make inferences about expected annual production and yield we first corrected each estimate of α for the difference between the median and mean of the lognormal error distribution from an AR(1) process (Parken et al. 2006):

$$\ln(\alpha') = \ln(\alpha) + \frac{\sigma_R^2}{2(1 - \varphi^2)} \quad (18)$$

The escapement that would generate maximum sustainable yield (S_{msy}) was approximated by (Hilborn 1985):

$$S_{msy} \cong \frac{\ln(\alpha')}{\beta} [0.5 - 0.07\ln(\alpha')] \quad (19)$$

Other relevant quantities include harvest rate (U_{msy}) leading to maximum sustained yield (MSY), approximated by (Hilborn 1985)

$$U_{msy} \cong \ln(\alpha') [0.5 - 0.07\ln(\alpha')] \quad (20)$$

escapement leading to maximum sustained recruitment (MSR)

$$S_{MSR} = \frac{1}{\beta} \quad (21)$$

and equilibrium spawning abundance, where recruitment exactly replaces spawners:

$$S_{EQ} = \frac{\ln(\alpha')}{\beta} \quad (22)$$

The probability that a given spawning escapement would produce average yields and recruitment exceeding 90% of MSY and MSR, respectively, was obtained by calculating yields and recruitment at incremental values of escapement for each MCMC sample, then comparing escapement with 90% of the value of MSY and MSR. The proportion of MCMC samples in which yield and recruitment exceeded 90% of MSY and MSR plotted against escapement are the optimal yield probability profile (OYP) and optimal recruitment probability profiles (ORP; Fleischman et al. 2013). The OYP and ORP were used to quantify the performance of the current SEG escapement goal, taking into consideration the uncertainty about the true abundance, productivity, and capacity of the stock.

Both the run reconstruction and stock recruitment models were analyzed using Bayesian methods with JAGS (Plummer 2003). JAGS was called from R (R Core Team 2018) using package R2jags (Su and Yajima 2015). Prior distributions on all unknown parameters were uninformative and their structures were based on recommendations from Fleischman et al. (2013) with necessary truncations to prevent the sampler from drawing implausible parameter values. For both models three parallel Markov chains, starting at random initial values in the range of parameter space, were run during 2,000,000 iterations and the initial convergence

phase was excluded by dropping the first 500,000 iterations to ensure convergence. We used the Brooks-Gelman-Rubin criterion \hat{R} (Brooks and Gelman 1998) and diagnostic plots to assess the convergence of chains to a stationary distribution. Model code for this analysis is found in appendices one and two.

RESULTS

Our modeling approach provided a realistic assessment of age structured escapement, harvest, run, recruitment and population dynamics parameters, in the presence of measurement error, serial correlation, and missing data. Empirical estimates for the run reconstruction and SRR are summarized below.

RUN RECONSTRUCTION

Runs, harvests and escapements all peaked during 2004 and have remained diminished since (Figure 2; Table 1). Estimates of escapement derived from mixed stock estimates (Smith and Liller 2018) were much less precise (1993–1995, and 2005; CV = 0.17–0.25, Figure 1) than those from direct observations and estimated missing daily passage (1992, 1996–2004, 2006–2017, and 2005; CV = 0.00–0.07, Figure 2). Harvest estimates from the application of the mixed stock harvest rates generally had low precision and are the major source of uncertainty in the total run and recruitment estimates. Coefficients of variation for recruitment were 0.20 or lower except when direct observations of escapement were unavailable (Figures 1 and 2).

The estimated median harvest rate on Kwethluk Chinook Salmon ranged mostly between 20% and 50% of total run abundance from 1992 to 2013, and has been greatly reduced since 2013 (Figure 1). Kwethluk Chinook Salmon age compositions were variable across years and among data type and were composed primarily of age-4 (1.2), age-5 (1.3), and age-6 (1.4) fish (Figure 2; Appendix 2). The age specific harvest rates indicate that harvest of Kwethluk Chinook Salmon was consistently selective for older age fish (age-6 and 7), with rates often exceeding twice that of younger fish (age-4; Figure 2).

STOCK-RECRUITMENT

The Ricker SRR is depicted in Figure 3. Posterior medians and credibility intervals for key model parameters are summarized in Appendix 3. The Ricker recruitment residuals (Figure 4) are deviations in recruitment from that predicted by the Ricker SR relationship, reflecting time-varying changes in productivity after controlling for density effects. The productivity of the stock reached a high in the 1999 brood year, then declined steadily until rebounding slightly for the 2009–2010 brood years. Escapement leading to maximum sustained yield was estimated to be 5,022 (95% CI: 2,524–7,710) fish. The optimal yield profile (Figure 5) is relatively steep and reached an elevated maxima (> 80%) indicating some certainty about yield dynamics. The lower and upper ends of the current escapement goals are near the maxima of the optimal yield and recruitment profiles, respectively. The lower end of the current SEG (4,100 fish) has at least a 0.84 probability of yielding 90% of MSY over the long term. The upper end of the current SEG (7,500 fish) has at least a 0.57 probability of yielding 90% of MSR over the long term.

DISCUSSION

We fit a Ricker SRR model to Kwethluk River Chinook Salmon data in order to learn about the yield and recruitment dynamics of this stock and validate current management objectives. The Kuskokwim River salmon management plan establishes a Sustainable Escapement Goal (SEG) of 4,100 – 7,500 Chinook Salmon for the Kwethluk River (Conitz et al. 2016). The state of Alaska policy is to set escapement goals that provide for sustained yield (5 AAC 39.220), but factors other than maximum yield are also important to consider. Current management considerations for population diversity and subsistence needs have also been identified (ANILCA 1980; USFWS 1992; 5 AAC 39.222(c)(2)(d)).

For subsistence fishers, run size maybe an important additional consideration because it affects catch rates. Run size is directly tied to recruitment, which reaches a maximum (MSR) at $S_{MSR} = 1/\beta$. By increasing the probability of reaching MSR we reduce the amount of effort needed to fulfill annual substance needs. Information about the range of escapements that lead to near-maximum recruitment is summarized in optimal recruitment profiles (Figure 8). The probability of achieving recruitment near MSR reaches a maximum at S_{MSR} and declines for lower and higher escapements. Conversely, the optimal yield profile (Figure 8) provides information about the range of escapements that produce near-maximum yields. The probability of achieving yields near MSY reaches a maximum at S_{MSY} and declines for lower and higher escapements. Under a Ricker spawner-recruit model, S_{MSR} is always higher than S_{MSY} , and thus, as you shift the management objectives away from yield and toward recruitment spawning escapements will increase.

The ideal escapement is one that would increase the probability of achieving MSR, thus increasing catch ability, while having a limited effect on yield. The current SEG of 4,100 – 7,500 Chinook Salmon for the Kwethluk River spans the tradeoff between the competing management objectives remarkably well, maximizing yields on the lower end of the goal while nearly reaching the recruitment maxima on the upper end. These results support the conclusions of Clark et al. (2014) about the validated appropriateness of quantile based SEGs as biological reference points. Therefore, we believe that escapement levels for Kwethluk River Chinook Salmon are set at sound levels and we recommend no change in current policy.

In addition to specific escapement goal ranges, the application of harvest strategies should ensure that the demographics (e.g. size range, sex ratio, age at maturity, and geographic and temporal distribution) of the population are maintained. Altering the structure of a fish population toward younger and thus smaller fish can lead to decreased fecundity (Walsh et al. 2006), lowered reproductive rates (Venturelli et al. 2009), loss of yield (Conover and Munch 2002), increased variability in abundance (Hsieh et al. 2006), and ultimately fishery collapse (Olsen et al. 2004).

Later maturing (ages 6, and 7) fish have been consistently exploited at rates greater than early maturing (age 4) fish (22 of the last 26 years; Figure 2). Harvest of age seven and six

fish were estimated at rates of up to 70% and 96%, respectively, in 2004, a rate well above U_{msy} (Figure 2). This disproportional level of harvest reduces the contribution of later maturing fish to the escapement. Because early maturation is highly heritable (Hard et al. 1985; and Hard et al. 2008), it seems plausible that selective harvest of older fish may skew the populations' genetic pre-disposition towards younger fish. Since 2013, when the run did not materialize, significant conservation measures have been implemented in the subsistence fishery to meet and improve the quantity and quality of escapements for Chinook Salmon. These restrictions have included time, area and gear (net size) restrictions (e.g. 3-S-WR-11-17 and 3-S-WR-01-18). The implementation of these restrictions appears to have had an effect, as the harvest rates in recent years are the lowest on record (Smith and Liller 2018), and harvest rates of older Chinook Salmon have plummeted reversing the age selectivity in the fishery. With this evidence for success we recommend a continued application of these strategies.

Acknowledging the large observation and process variation in this analysis we recommend that these reference points continue to be applied conservatively. Our knowledge of Kwethluk River Chinook Salmon stock dynamics will improve over time. Lacking a complete time series of stock specific estimates of harvest and escapement, this investigation relied partially upon indirect reconstruction of past quantities. For our spawner-recruit analyses, we employ statistical methods that accommodate varying levels of measurement error and give greater weight to more precise estimates. As precise estimates of abundance accumulate, they will contribute a greater share of the information about S_{MSY} and S_{MSR} , while historical, indirect estimates of abundance will naturally have less influence. To reduce the greatest amount of uncertainty we recommend estimating stock specific harvest directly. This analysis highlights the irreplaceable value of long-term data sets, providing insight into the changing dynamics of the population and allow for the assessment of management actions. Therefore, it is strongly recommended that the operation of these assessment projects continue.

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Table 1.—Point estimates (posterior medians) and coefficients of variation (CV) of spawning escapement, harvest, total run abundance, and recruitment, for Kwethluk River Chinook Salmon, 1992–2017.

Year	Escapement (CV)	Harvest (CV)	Run (CV)	Recruitment (CV)
1992	9,675 (0.00)	6,612 (0.55)	16,287 (0.23)	13,549 (0.18)
1993	10,869 (0.22)	4,637 (0.71)	15,698 (0.31)	8,805 (0.25)
1994	16,235 (0.25)	6,144 (0.83)	22,801 (0.35)	8,244 (0.16)
1995	14,562 (0.22)	6,280 (0.71)	21,071 (0.31)	8,457 (0.25)
1996	10,244 (0.04)	3,949 (0.75)	14,213 (0.24)	12,759 (0.15)
1997	11,892 (0.02)	4,015 (0.73)	15,914 (0.21)	12,946 (0.12)
1998	5,640 (0.31)	4,114 (0.86)	9,944 (0.49)	17,446 (0.16)
1999	1,522 (0.07)	967 (0.67)	2,496 (0.29)	22,780 (0.12)
2000	3,641 (0.02)	2,842 (0.50)	6,495 (0.22)	34,914 (0.11)
2001	9,061 (0.21)	3,680 (0.69)	12,887 (0.29)	23,196 (0.16)
2002	9,073 (0.02)	3,995 (0.55)	13,087 (0.18)	17,065 (0.19)
2003	14,474 (0.00)	4,463 (0.58)	18,937 (0.14)	13,518 (0.19)
2004	27,696 (0.01)	8,525 (0.60)	36,227 (0.15)	7,761 (0.18)
2005	15,575 (0.17)	4,491 (0.58)	20,169 (0.21)	6,574 (0.18)
2006	17,899 (0.03)	6,451 (0.60)	24,408 (0.17)	4,230 (0.21)
2007	13,314 (0.01)	6,656 (0.45)	19,988 (0.15)	3,436 (0.19)
2008	6,241 (0.04)	4,599 (0.46)	10,852 (0.20)	2,606 (0.24)
2009	6,474 (0.03)	4,030 (0.49)	10,510 (0.20)	4,997 (0.24)
2010	1,743 (0.02)	2,028 (0.39)	3,774 (0.21)	7,191 (0.22)
2011	3,779 (0.00)	3,285 (0.42)	7,064 (0.20)	—
2012	1,232 (0.04)	378 (0.71)	1,616 (0.19)	—
2013	1,076 (0.06)	1,098 (0.39)	2,176 (0.21)	—
2014	3,315 (0.01)	607 (0.78)	3,926 (0.14)	—
2015	8,139 (0.00)	1,613 (0.79)	9,752 (0.16)	—
2016	5,798 (0.25)	1,494 (0.80)	7,484 (0.30)	—
2017	7,980 (0.03)	1,441 (0.77)	9,436 (0.14)	—

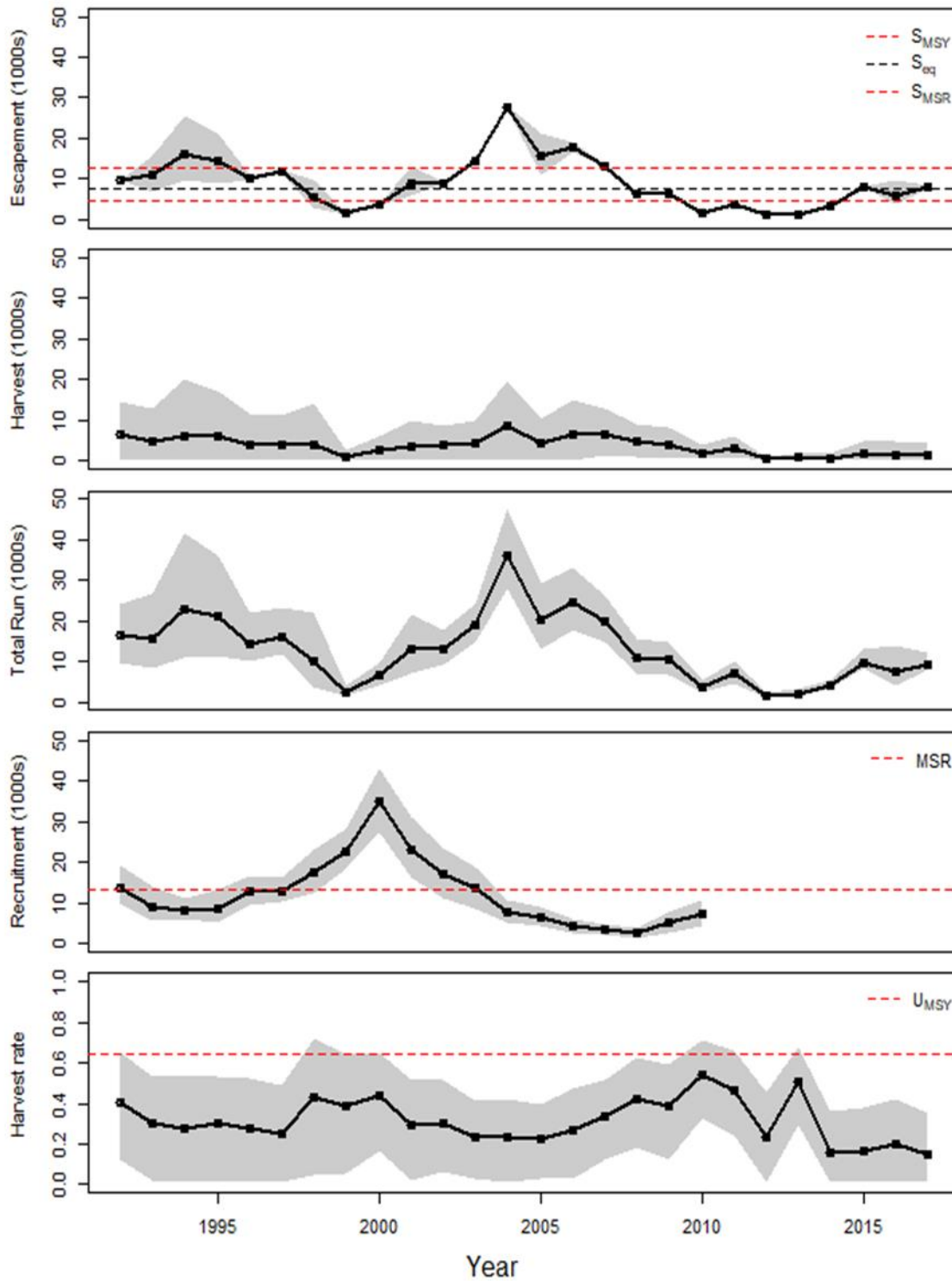


Figure. 1. Point estimates (black dots) and 95% credibility intervals (gray bands) of spawning escapement, harvest, run abundance, recruitment by brood year, and harvest rate for Kwethluk River Chinook Salmon, 1992–2017. Posterior medians of S_{MSY} , S_{EQ} , S_{MSR} , MSR and U_{MSY} are plotted as dashed horizontal reference lines.

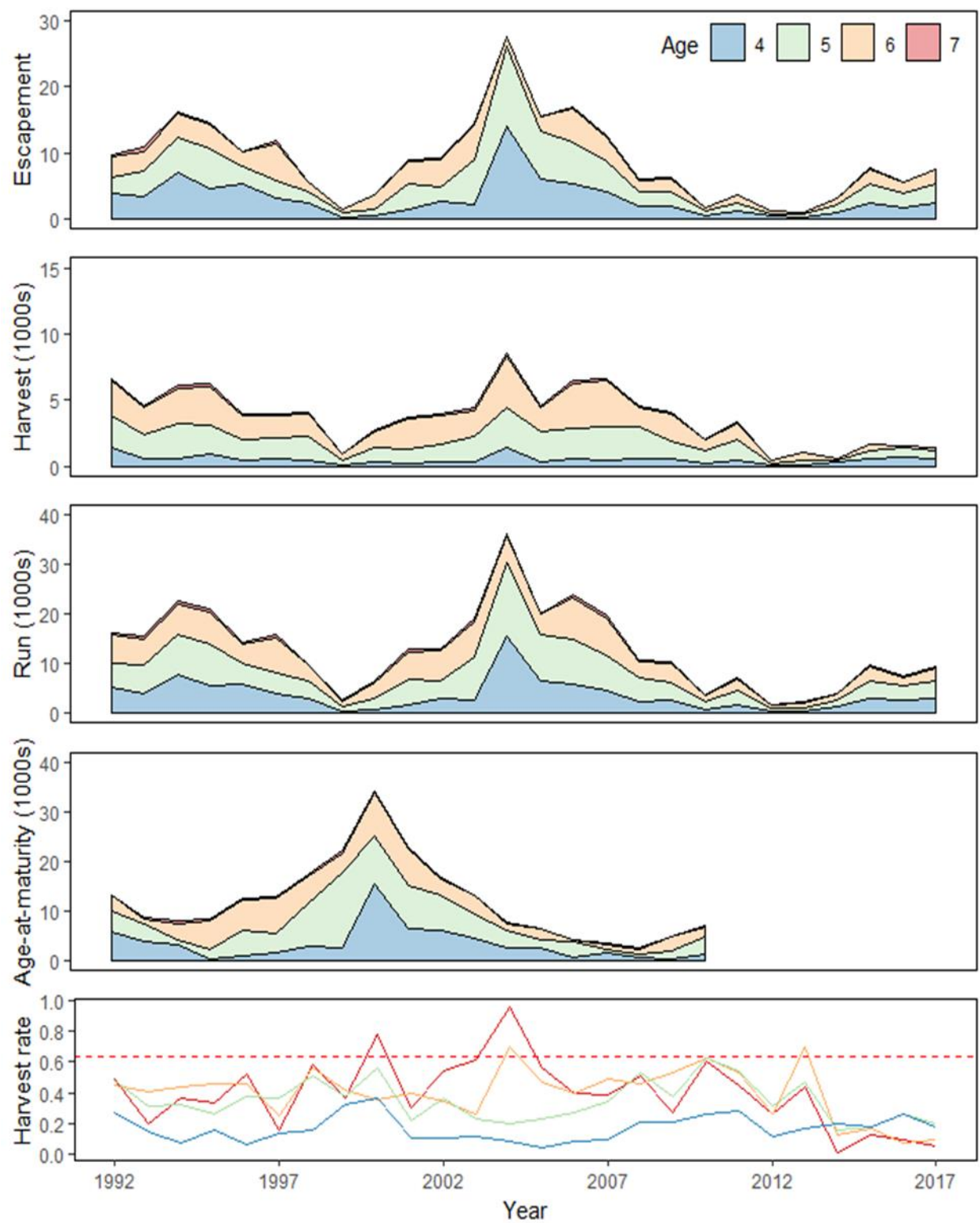


Figure 3. Age structured spawning escapement, harvest, run abundance, recruitment by brood year, and harvest rate for Kwethluk River Chinook Salmon, 1992–2017. The posterior median of U_{MSY} is plotted as a red dashed horizontal reference line.

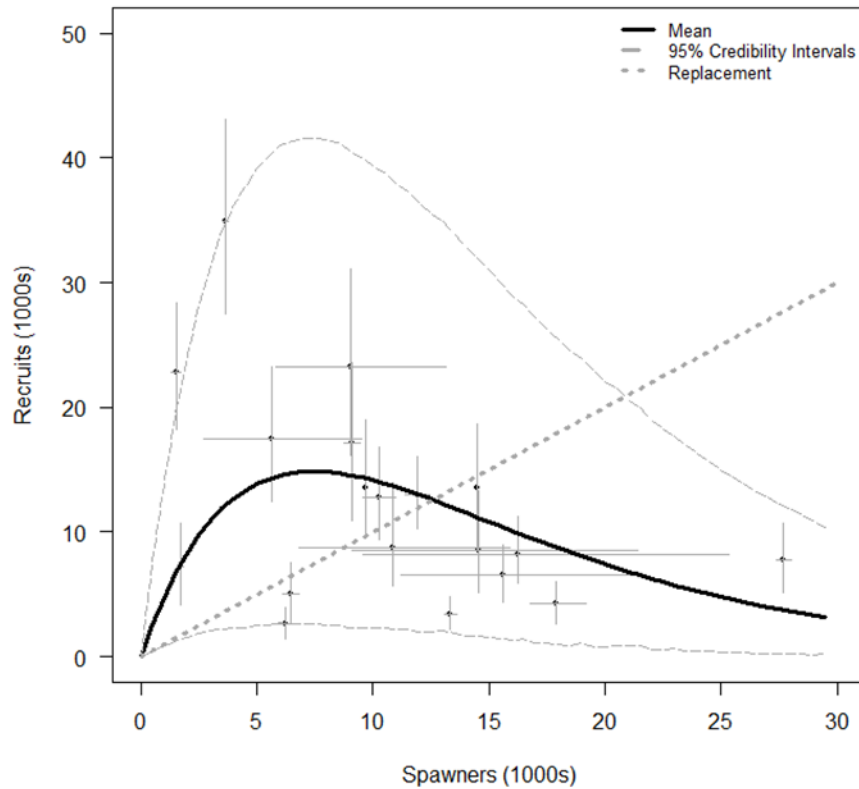


Figure 3. Ricker modeled spawner-recruit relationship for Kwethluk River Chinook Salmon, brood years 1992–2010. Error bars on points represent the 95% Bayesian credibility intervals on brood year linked escapement and recruitment and long dashed gray curves are 95% Bayesian credibility intervals for predicted recruitment given stock size. The dashed line represents 1:1 replacement.

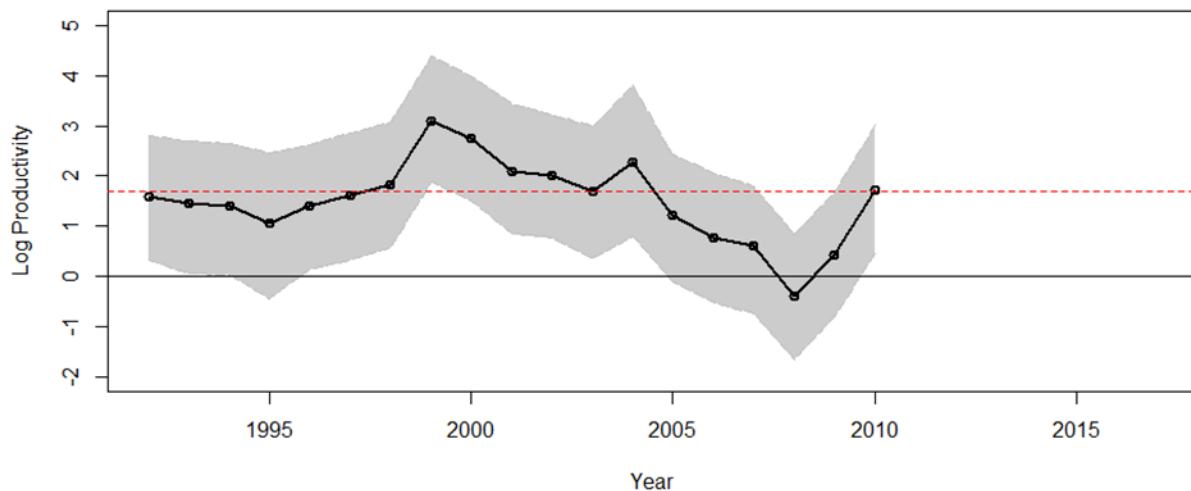


Figure 4. Annual values of time-varying (log) productivity for Kwethluk River Chinook Salmon, brood years 1992–2010. Mean log productivity, corrected for lognormal production, is represented by the red horizontal reference line.

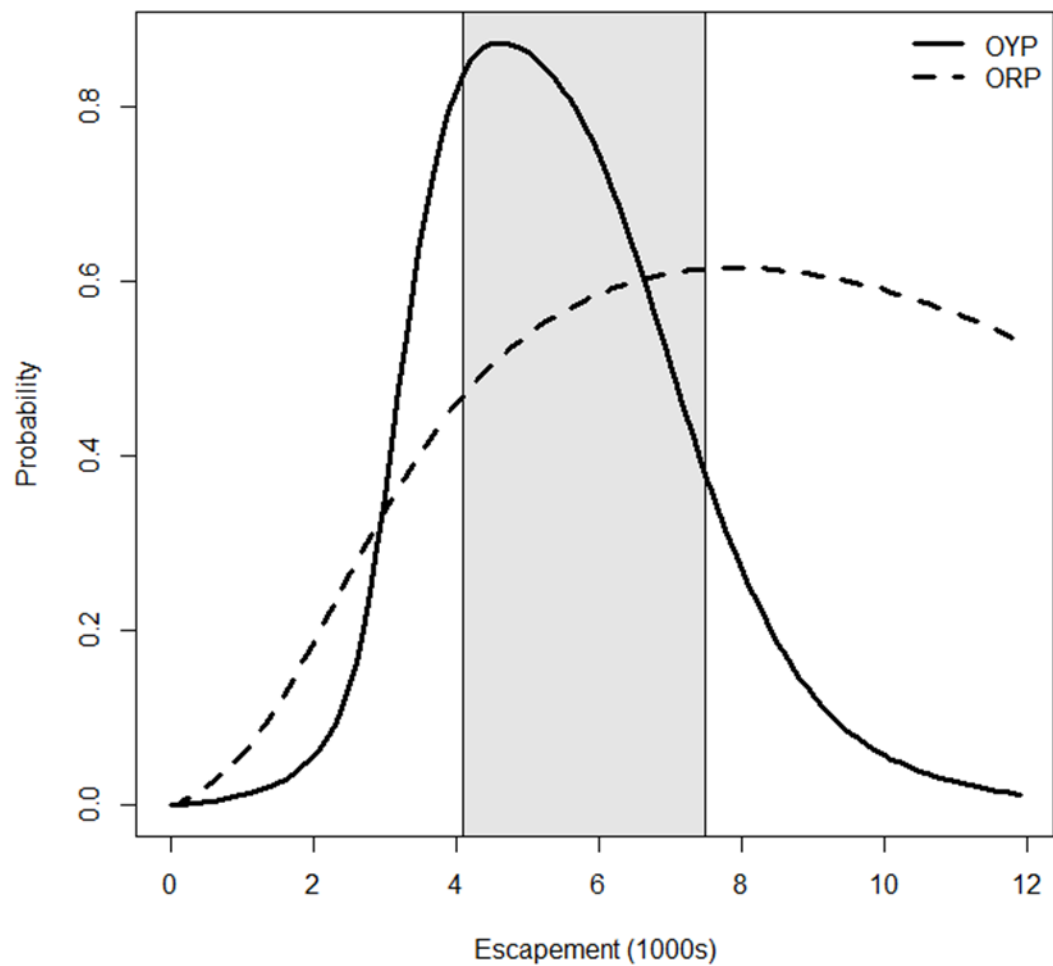


Figure 5.—Optimal yield profile (OYP), and optimal recruitment profile (ORP) for Kwethluk Chinook Salmon. The OYP and ORP show the probability that a specified spawning abundance will result in 90% of maximum sustained yield and 90% of maximum recruitment. The shaded area brackets the current SEG goal range (4,100, 7,500 fish).

Appendix A.—RJAGS model code for a Run reconstruction of Kewthluk River Chinook Salmon, 1992–2017.

```
#####
#### estimate Spawning Escapements#####
#### log normal run timing model for missed passage see Liller and Head 2016#####
#####
# LIKELIHOOD
for(j in 1:nyrs) {
  for(i in 1:ndays){
    y[j,i] ~ dnorm(theta[j,i], tausq[j])T(0,)
    log(theta[j,i]) <- a[j]*exp(-0.5*pow(log(x[i]/mu[j])/b[j],2))
  }
}
# PRIORS
for(i in 1:nyrs) {
  a[i] ~ dnorm(0,0.01)T(0,)#maximum height (amplitude)
  b[i] ~ dnorm(b0,b0.prec)T(0,)#peak width (SD)
  mu[i] ~ dnorm(mu0,mu0.prec)T(0,)#Peak timing
}
b0 ~ dnorm(0.5,0.01)T(0,)
mu0 ~ dnorm(50,0.01)T(0,)
b0.prec <- 1/b0.ssq
b0.ssq <- b0.sigma*b0.sigma
b0.sigma ~ dunif(0,100)
mu0.prec <- 1/(mu0.sigma*mu0.sigma)
mu0.sigma ~ dunif(0,100)

## variance of each year is independent.
for(i in 1:nyrs) {
  tausq[i] <- pow(sigma[i],-2)
  sigma[i] ~ dunif(0,100)
}
# Derived quantities
for(j in 1:nyrs){
  ##Estimate Escapement for years with obs
  s_obs[j]<-sum(y[j,])
}
#####
##Estimate Escapement for years with no obs using the relationship of the Kwe and the mixed stock....
#see Smith and Liller 2018 #####
#####
Kwe.ScalingParm ~ dnorm(19.3,0.171)T(0,)
for(j in 1:length(MSRR)){
  sigma.MSRR[j] <- sqrt(log(pow(MSRR.CV[j],2)+1))
  tau.log.MSRR[j] <- 1/pow(sigma.MSRR[j],2)
  log.MSRR[j] <- log(MSRR[j])
  Kusko[j] ~ dlnorm(log.MSRR[j],tau.log.MSRR[j])
  s_est[j] <- Kusko[j]/Kwe.ScalingParm
}
##make new vector with est from the observed data and Kusko RR fraction for years with no observations
for(j in 1:length(estyear)){
  s[estyear[j]]<-s_est[j]
}
for(j in 1:length(obsyear)){
  s[obsyear[j]]<-s_obs[j]
}
}
```

Appendix A.– continued

```
#####
##Estimate Escapement age structure using a conditional dirichlet-multinomial #####
#####

#explicit conditional age probabilities
pi[1] <- prob[1]
pi[2] <- prob[2] * (1 - pi[1])
pi[3] <- prob[3] * (1 - pi[1] - pi[2])
pi[4] <- 1 - pi[1] - pi[2] - pi[3]
# LIKELIHOOD
for (y in 1 : Y) {
  X[y,1:A] ~ dmulti(q[y,1:A], n[y])
  for (a in 1:A) {
    gamma[y,a] <- D.sum * pi[a]
    g[y,a] ~ dgamma(gamma[y,a],1)
    obs_p[y,a] <- g[y,a]/sum(g[y,])
    q[y,a] <- esc_A[y,a]/sum(esc_A[y,])
  }
}
# PRIORS
D.scale ~ dunif(0,1)
D.sum <- 1 / (D.scale * D.scale)
prob[1] ~ dbeta(1,1)
prob[2] ~ dbeta(1,1)
prob[3] ~ dbeta(1,1)
##Age structure predictions for missing years###
for(y in 1:N) {
  for(a in 1:A) {
    est_p[y,a] <- est_g[y,a] / sum(est_g[y,])
    est_gamma[y,a] <- D.sum * pi[a]
    est_g[y,a] ~ dgamma(est_gamma[y,a],1)
  }
}
##make new vector with observed age data and projections for years with no observations
for(a in 1:A) {
  for(y in 1:N){
    pr[Age_est_ID[y],a]<-est_p[y,a]
  }
  for(y in 1:Y){
    pr[Age_obs_ID[y],a]<-obs_p[y,a]
  }
}
for (a in 1 : A) {
  for(y in 1:allyr) {
    esc_A[y,a]<- s[y]*pr[y,a]
  }
}

#####
##Predict Kwe River specific harvest using the mixed stock exploitation rates as a proxy #####
##this assumes that there is not selective harvest among stocks #####
#####
for(y in 1:allyr) {
  Kusko_sigma[y] <- sqrt(log(pow(Kusko_CV[y],2)+1))
  Kusko_tau[y] <- 1/pow(Kusko_sigma[y],2)
}
```

Appendix A.– continued

```

log_Kusko_RUN[y] <-log(Kusko_RUN[y])
RUN[y] ~ dlnorm(log_Kusko_RUN[y],Kusko_tau[y])
Kusko_ESC[y] ~ dlnorm(log(RUN[y] * (1-Kwe_U[y])),Kusko_tau[y])
Kwe_U[y] ~ dunif(0.01, 0.99)
Kwe_H[y]<- (s[y]/(1-Kwe_U[y]))*Kwe_U[y]
}

#####
##Harvest Age Structure#####
##ADFG data from Liller (Nov 17 2018) #####
#####

#explicit conditional age probabilities
H_pi[1] <- H_prob[1]
H_pi[2] <- H_prob[2] * (1 - H_pi[1])
H_pi[3] <- H_prob[3] * (1 - H_pi[1] - H_pi[2])
H_pi[4] <- 1 - H_pi[1] - H_pi[2] - H_pi[3]

# LIKELIHOOD
for (a in 1:A){
  H_gamma[a] <- H_D.sum * H_pi[a]
}
for (y in 1:allyr){
  HA[y,1:A] ~ dmulti(H_q[y,1:A] , H_n[y])
  for (a in 1:A){
    H_g[y,a] ~ dgamma(H_gamma[a],1)
    H_p[y,a] <- H_g[y,a]/sum(H_g[y,])
    H_q[y,a] <- H_A[y,a]/sum(H_A[y,])
  }
}
# PRIORS
H_D.scale ~ dunif(0,1)
H_D.sum <- 1 / (H_D.scale * H_D.scale)
H_prob[1] ~ dbeta(1,1)
H_prob[2] ~ dbeta(1,1)
H_prob[3] ~ dbeta(1,1)

for (y in 1:allyr) {
  for (a in 1:A) {
    H_A[y,a] <- Kwe_H[y] * H_p[y,a]
  }
}

#####
##Run#####
#####

for(y in 1:allyr) {
  for (a in 1:A) {
    Run_A[y,a] <-esc_A[y,a]+H_A[y,a]
  }
  Run[y] <- sum(Run_A[y,])
}

#####
###Return#####
#####

```

Appendix A.– continued

```
#Brood table##
  R_A[1:(allyr-7),1] <- Run_A[5:(allyr-3),1]
  R_A[1:(allyr-7),2] <- Run_A[6:(allyr-2),2]
  R_A[1:(allyr-7),3] <- Run_A[7:(allyr-1),3]
  R_A[1:(allyr-7),4] <- Run_A[8:(allyr),4]
  for(y in 1:(allyr-7)) {
    R[y] <- sum(R_A[y,])
  }
#####
## U #####
#####
  for(y in 1:allyr) {
    for (a in 1:A) {
      U_A[y,a] <- H_A[y,a]/Run_A[y,a]
    }
    U[y] <- Kwe_H[y]/Run[y]
  }
}"END
```


Appendix B.—RJAGS model code for Ricker spawner recruit model of Kewthluk River Chinook Salmon, 1992–2017.

```
#####
# AR[1] STOCK-RECRUITMENT model specification#####
#####
"data{
##Import point estimates and CV's from the run reconstruction
for(y in 1:Y) {
  S_sigma[y] <- sqrt(log(pow(S_CV[y],2)+1))
  S_tau[y] <- 1/pow(S_sigma[y],2)
  R_sigma[y] <- sqrt(log(pow(R_CV[y],2)+1))
  R_tau[y] <- 1/pow(R_sigma[y],2)
  log_est_R[y] <-log(est_R[y])
  log_est_S[y] <-log(est_S[y])
  S.temp[y] ~ dlnorm(log_est_S[y],S_tau[y])
  R.temp[y] ~ dlnorm(log_est_R[y],R_tau[y])
  Ln.R[y] <-log(R.temp[y])
  S[y] <- S.temp[y]
}
}
model{
# priors
Ln.alpha ~ dnorm(0,1.0E-6)l(0,5)
beta ~ dunif(1.0E-4,1)
phi ~ dnorm(0,1.0E-6)l(-1,1)
R.tau ~ dgamma(0.01,0.01)
R0.tau <- R.tau*(1-phi*phi)
Ln.resid.0 ~ dnorm(0,R0.tau)
# likelihood
for(y in 1:Y) {
  Ln.R[y] ~ dt(Ln.R.mu[y], R.tau,500)
  R[y]<-exp(Ln.R[y])
  Temp.Ln.R.mu[y] <- log(S[y])+Ln.alpha-beta*S[y] # Ricker 1954
  Ln.resid[y]<- log(R[y])-Temp.Ln.R.mu[y]
  resid[y]<- exp(Ln.resid[y])
  Ln.alpha.y[y]<-Ln.resid[y]+Ln.alpha
  alpha.y[y]<- exp(Ln.alpha.y[y])
}
Ln.R.mu[1] <- Temp.Ln.R.mu[1]+phi*Ln.resid.0
for(y in 2:Y) {
  Ln.R.mu[y]<-Temp.Ln.R.mu[y]+phi*Ln.resid[y-1]
}
sigma.R <- 1/sqrt(R.tau)
alpha <- exp(Ln.alpha)
Ln.alpha.cor <- Ln.alpha+((sigma.R^2)/2*(1-(phi^2))) # correct lognormal skew # Parken et al. 2006
S.max <- 1/beta
S.eq <- Ln.alpha.cor*S.max
S.msy <- S.eq*(0.5-0.07*Ln.alpha.cor) # Hilborn 1985
U.msy <- Ln.alpha.cor*(0.5-0.07*Ln.alpha.cor)
R.msy <- S.msy * exp(Ln.alpha.cor - beta * S.msy)
R.max <- S.max * exp(Ln.alpha.cor - beta * S.max)
MSY <- R.msy - S.msy
# Predicted R and y given S:
for (y in 1:length(S2)) {
  R.Pred[y] <- min(S2[y] * exp(Ln.alpha.cor - beta * S2[y]),1.0E6)
  Y.Pred[y] <- R.Pred[y]-S2[y]
  oyp[y]<- step(Ln.alpha.cor)*step(Y.Pred[y]-MSY*0.9)
}
}
```

Appendix C. Model parameter estimates for a run reconstruction and stock-recruit analysis of Kwethluk River Chinook Salmon 1992–2017.

Parameter	Median	0.05 percentile	0.95 percentile	CV
$\ln(\alpha')$	1.69	0.40	2.99	0.37
α	4.7	1.0	14.4	0.67
β	1.31E-04	1.00E-04	1.78E-04	0.17
ϕ	0.69	0.36	0.99	0.25
σ_R	0.66	0.46	0.93	0.18
S_{MSR}	7,648	5,604	9,999	0.16
S_{EQ}	12,576	2,610	22,053	0.36
S_{MSY}	4,728	2,102	7,323	0.26
U_{MSY}	0.64	0.33	0.89	0.25
Harvest D	21.25	14.32	28.86	0.17
Harvest π_4	0.14	0.12	0.17	0.10
Harvest π_5	0.42	0.37	0.46	0.05
Harvest π_6	0.40	0.35	0.44	0.05
Harvest π_7	0.04	0.03	0.06	0.17
Escapement D	13.79	7.84	20.57	0.24
Escapement π_4	0.31	0.25	0.37	0.10
Escapement π_5	0.36	0.29	0.42	0.09
Escapement π_6	0.29	0.23	0.35	0.11
Escapement π_7	0.04	0.02	0.07	0.27
a_1	6.41	6.28	6.55	0.01
a_2	6.54	6.34	6.74	0.02
a_3	7.03	6.91	7.16	0.01
a_4	5.43	4.95	8.86	0.31
a_5	5.28	5.00	5.51	0.02
a_6	6.03	5.87	6.18	0.01
a_7	6.55	6.46	6.64	0.01
a_8	7.26	7.21	7.30	0.00
a_9	6.83	6.74	6.91	0.01
a_{10}	6.57	6.47	6.67	0.01
a_{11}	5.41	4.96	6.43	0.07
a_{12}	5.78	5.55	6.01	0.02
a_{13}	4.21	3.89	4.49	0.04
a_{14}	5.31	5.16	5.45	0.01

Appendix 2. continued

Parameter	Median	0.05 percentile	0.95 percentile	CV
a_{15}	5.36	5.28	5.45	0.01
a_{16}	3.61	3.04	4.09	0.08
a_{17}	5.32	5.19	5.45	0.01
a_{18}	5.72	5.52	5.90	0.02
a_{19}	5.72	5.26	6.41	0.06
a_{20}	5.86	5.66	6.05	0.02
b_1	0.72	0.61	0.83	0.08
b_2	0.40	0.30	0.53	0.15
b_3	0.27	0.23	0.32	0.08
b_4	0.03	0.01	0.05	0.35
b_5	0.52	0.36	0.68	0.15
b_6	0.91	0.71	1.11	0.11
b_7	1.00	0.91	1.09	0.05
b_8	1.26	1.20	1.32	0.03
b_9	0.94	0.81	1.08	0.07
b_{10}	0.72	0.64	0.80	0.06
b_{11}	0.67	0.07	0.92	0.42
b_{12}	0.57	0.41	0.74	0.15
b_{13}	0.55	0.31	0.75	0.22
b_{14}	0.62	0.51	0.72	0.09
b_{15}	0.17	0.16	0.19	0.05
b_{16}	0.53	0.24	0.76	0.25
b_{17}	0.74	0.63	0.85	0.08
b_{18}	0.97	0.79	1.16	0.10
b_{19}	0.75	0.54	0.97	0.15
b_{20}	0.64	0.49	0.80	0.12
μ_1	16.80	16.04	17.61	0.02
μ_2	16.31	15.79	16.85	0.02
μ_3	15.51	15.24	15.77	0.01
μ_4	30.13	29.77	30.47	0.01
μ_5	22.62	20.36	24.85	0.05
μ_6	16.99	15.01	18.83	0.06
μ_7	17.53	16.66	18.43	0.03
μ_8	13.83	13.41	14.26	0.02

Appendix 2. continued

Parameter	Median	0.05 percentile	0.95 percentile	CV
μ_9	17.23	15.99	18.34	0.04
μ_{10}	21.62	20.87	22.38	0.02
μ_{11}	20.21	17.46	24.13	0.09
μ_{12}	21.96	20.28	23.58	0.04
μ_{13}	24.78	20.42	29.22	0.10
μ_{14}	23.19	21.74	24.70	0.03
μ_{15}	18.36	18.21	18.50	0.00
μ_{16}	19.02	15.61	23.25	0.10
μ_{17}	14.76	13.97	15.55	0.03
μ_{18}	18.86	16.14	21.87	0.08
μ_{19}	19.51	14.48	23.79	0.12
μ_{20}	23.83	21.64	25.95	0.05
w_1	97.79	92.19	100.00	0.03
w_2	98.83	95.32	100.00	0.02
w_3	99.39	97.44	100.00	0.01
w_4	20.88	17.07	25.55	0.10
w_5	63.16	53.79	74.50	0.08
w_6	96.36	88.67	100.00	0.04
w_7	99.73	98.87	100.00	0.00
w_8	99.93	99.71	100.00	0.00
w_9	99.63	98.41	100.00	0.01
w_{10}	99.35	97.32	100.00	0.01
w_{11}	95.60	86.48	100.00	0.04
W_{12}	81.49	91.79	100.00	0.06
W_{13}	21.85	26.13	31.00	0.09
W_{14}	36.09	42.32	49.57	0.08
W_{15}	9.50	11.43	13.69	0.09
w_{16}	12.72	15.75	19.24	0.11
w_{17}	26.80	31.63	37.18	0.08
W_{18}	92.89	98.06	100.00	0.02
W_{19}	16.27	20.12	24.51	0.11
W_{20}	89.22	96.66	100.00	0.04

Chapter 3

Chinook Salmon Population-level Responses to Weather Anomalies During Spawning and Incubation, Kwethluk River, Alaska.

ABSTRACT

Chinook Salmon (*Oncorhynchus tshawytscha*) populations across the Arctic-Yukon-Kuskokwim (AYK) Region have experienced declines in abundance and productivity. The life phase and the variables driving these declines are uncertain. We hypothesize that changes in Kwethluk River Chinook Salmon productivity are linked to divergent environmental regimes during the fall spawning and incubation period. We used a stock-recruitment model to investigate brood year fall precipitation and air temperature anomalies as drivers of Chinook population productivity in the Kwethluk River. Above average brood year fall temperature and precipitation negatively affect productivity (e.g. a daily average increase of 1°C and 0.1 cm above the average fall temperature and precipitation results in a 50% reduction in productivity). Indicating that above optimal temperatures and flooding during the early life stages may be important factors driving the productivity of Chinook Salmon populations in the Kwethluk River.

INTRODUCTION

Chinook Salmon population-level responses to environmental variation are common and have been identified across the North Pacific (Ohlberger et al. 2016). These responses may occur at one or more points in ontogenetic development (Quinn and Deriso 1999) and may have location-specific impacts (Ohlberger et al. 2016). Identifying the population specific period(s) and variable(s) that account for significant amounts of variation in productivity may provide managers and stakeholders with pragmatic expectations and guidance when responding to depressed Chinook Salmon stocks (Peterman et al. 2009).

During the recent down turn in Chinook Salmon productivity, climate records for the Yukon-Kuskokwim delta, measured at the Bethel airport, show above average temperature and rain events. In fact during the 2003 – 2010 period, fall¹ maximum temperatures exceeded the long term average (1992–2010) for all but one year (NCEI 2017; 1992-2010). Rain fall totals were also exceptional, exceeding the average 57% of the time (NCEI 2017; 1992-2010). These warmer wetter conditions may have affected the suitability of freshwater habitats for the Chinook Salmon that produced recent returns.

In Stream temperatures and flows, can have significant effects on Salmon and their habitats, and are associated with productivity of other Western and Interior Alaskan Chinook Salmon populations (Neuswanger et al. 2015, Ohlberger et al. 2016, Cunningham et al.

¹fall is defined as the time between the estimated annual median spawning date and the beginning of freeze up (minimum air temperatures at the Bethel airport < 0 °C).

2018). In unstable environments inter and intra-specific competition and predation become less important as population regulators (Schindler et al. 2005, Lawrence et al. 2014; and Schoen et al. 2015). Spawn timing, fry emergence, and smolting are largely driven by temperature (Quinn 2005). The emergence period is selected to correspond with ideal temperatures (Skoglund et al., 2011; and Beer and Steel 2018) and has direct implications to condition (Fuhrman et al., 2018) and fitness (Einum and Fleming, 2000). Flooding events cause eggs and fry to be dislodged and sedimentation of spawning redds decreasing egg-to-fry survival (Beamer et al. 2005). Changes in flood frequencies and increased temperatures have the potential to significantly alter the suitability of freshwater habitats.

Previous work with Kwethluk River Chinook Salmon has identified changes in freshwater productivity potentially linked to differing temperature regimes during the fall spawning and incubation period (chapter 1). We hypothesize that this relationship is a significant driver of adult recruitment. We compiled run reconstruction estimates (chapter 2), precipitation, and air temperature data (NCDC 2017; 1992-2010) to test this hypothesis.

METHODS

To model the effect of fall temperature and precipitation anomalies on the productivity of Kwethluk River Chinook Salmon we employed a Bayesian spawner-recruit model that assumes a Ricker Spawner recruit relationship (Ricker 1954) and incorporates environmental covariates. This model takes into account the pervasive uncertainties in the stock assessment data caused by imperfect data collection, temporal environmental variability, and outcome uncertainties. Simultaneously modeling process and observation error allows for a realistic depiction of the system dynamics and sampling design. The model treats run abundance estimates from the run reconstruction as independently observed data with fixed uncertainty captured in the CVs. This observation error is incorporated into the spawner-recruit model by specifying the relationship of observable data to the estimates of the individual stock-recruitment quantities.

Environmental covariates.— Brood year fall temperature anomalies were calculated, from bethel, airport data (NCEI 2017; 1992-2010) as the difference in the daily norms for annual fall minimum temperatures and the 19 year average (1992-2010). Similarly, fall precipitation anomalies were calculated as the difference in the daily norms for annual fall precipitation and the 19 year average. We chose to use average minimum fall temperatures because we wanted to capture the timing and magnitude of cooling during the fall period.

Stock—recruitment.— Returns of Kwethluk River Chinook Salmon from the 1992 – 2010 brood years (chapter 2) were modeled as a function of annual spawning escapement using a Ricker (1954) stock-recruitment model with an auto regressive (AR) lognormal process error (Fleischman et al. 2013). The base parameterization of the Ricker function is as follows:

$$\ln(R_y) = \ln(S_y) + \ln(\alpha) - \beta S_y + \phi\omega_{y-1} + \varepsilon_y \quad (1)$$

Where α is the productivity parameter, β is the (inverse) capacity parameter, φ is the AR lag-1 coefficient, ω_y is the model residual, and ε_y are the independent normally distributed process errors with standard deviation σ_R .

Environmental covariates were specified to have an additive effect on the log recruitment rate. Temperature (t) and precipitation (p) effects are drawn from a normal distribution:

$$t_y \sim \text{Normal}(\mu_{t_y}, \sigma_{t_y}^2) \text{ and} \quad (2)$$

$$p_y \sim \text{Normal}(\mu_{p_y}, \sigma_{p_y}^2) \quad (3)$$

where hyperparameters μ and σ describe the distribution of covariate effects on Kwethluk production.

Both the base and environmental covariate parameterizations were analyzed using Bayesian methods with JAGS (Plummer 2003). JAGS was called from R (R Core Team 2018) using package R2jags (Su and Yajima 2015). Prior distributions on all unknown parameters were uninformative and their structures were based on recommendations from Fleischman et al. (2013) with necessary truncations to prevent the sampler from drawing implausible parameter values (appendix 1). For both models three parallel Markov chains, starting at random initial values in the range of parameter space, were run during 2,000,000 iterations and the initial convergence phase was excluded by dropping the first 500,000 iterations to ensure convergence. We used the Brooks-Gelman-Rubin criterion \hat{R} (Brooks and Gelman 1998) and diagnostic plots to assess the convergence of chains to a stationary distribution. Goodness of fit diagnostic plots were analyzed using a maximum likelihood linear fits. Model code for this analysis is found in appendices A and B.

RESULTS

The base and environmental covariate parameterizations are depicted in Figure 1. Posterior medians and credibility intervals for key model parameters are summarized in Table 1. Average daily brood year fall precipitation anomalies ranged by 0.52 cm (Figure 2a). Average daily brood year fall minimum temperature anomalies ranged by 3.6 °C (Figure 2b).

The environmental covariate parameterizations fit the observed recruitment data reasonably well, explaining 82% of the total variation in productivity. Average daily precipitation anomalies during the fall spawning and incubation season were strongly negatively associated with productivity and accounting for 41% of the variability in productivity when controlling for spawning abundance (Figure 3a). Daily average minimum fall temperature during the spawning and incubation season was also strongly negatively associated with productivity and accounted 23% of the variability in productivity when controlling for spawning abundance (Figure 3b). Precipitation and temperature anomalies do not appear to be associated (Figure 3c).

DISCUSSION

Our hypothesis, that abnormal environmental conditions would be a significant driver of recruitment was verified. There were clear negative associations with productivity and higher than average precipitation rates and maximum temperature during the fall spawning and incubation period. Identifying the population specific period(s) and variable(s) that account for the observed variation in productivity is critical to adapting management strategies and expectations.

High precipitation rates during the fall spawning and incubation period had the strongest negative effect on Salmon productivity, indicating that flooding and scour may be important factors driving productivity of Chinook populations in the Kwethluk River. Heavy or extreme rain events causing high flow conditions during the spawning and incubation period may scour redds and reduce egg-to-fry survival (Beamer et al. 2005) negatively impacting recruitment.

Warmer than average maximum temperatures maybe acting on adult spawning success. High temperatures during the spawning migration can cause: delayed run timing (Bernatchez and Dodson 1985), increased straying (Hartman and Holtby 1982), decreased numbers of fertile eggs (Weber-Scannell 1991) and thermal stress and death (Richter and Kolmes 2005). Egg development, Fry emergence, and smolting are largely driven by temperature (Beacham and Murray 1990, Quinn 2005). The optimum temperature for egg incubation is relatively narrow (Weber-Scannell 1991). Chinook Salmon incubated at warmer temperatures have higher mortality, hatched and emerged precociously, and were smaller, at hatching, as alevines and as fry (Weber-Scannell 1991). This asymmetry maybe a driver of the observed declines in production.

Previous work in the Kwethluk River identified differing temperature regimes during the spawning and incubation periods indicating a differential in emergence timing. As maximum brood year fall temperatures increased the condition and production of migrating juvenile salmon decreased. Similarly, as parental spawning abundances increased the production and the condition of their progeny decreased (Chapter 1). While there are apparent density effects, climatic controls are outweighing density regulators during many brood years. These results are constant with many other Salmon stocks (Szuwalski et al., 2015).

By explaining a sizeable amount of the variability in production with environmental variables, which are realized during a brood year, allows managers to anticipate down turns in productivity before adults recruit (Ohlberger et al. 2016). Forecasting the effects of current or hypothesized changes in environmental variable can have mixed results for single stock models (Peterman et al. 2008). We therefore recommend that a multi-stock models (meta-analyses) be developed for the Kuskokwim basin to produce more precise and accurate preseason forecasts.

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Table 1. Model parameter estimates for a base (top) and environmental covariate (bottom) parameterizations of a Ricker stock-recruit relationship for Kwethluk River Chinook Salmon 1992–2017.

Parameter	Median	0.05 percentile	0.95 percentile	CV
α	4.7	1.0	14.4	0.67
β	1.31E-04	1.00E-04	1.78E-04	0.17
ϕ	0.69	0.36	0.99	0.25
σ_R	0.66	0.46	0.93	0.18
S_{MSR}	7,648	5,604	9,999	0.16
S_{EQ}	12,576	2,610	22,053	0.36
S_{MSY}	4,728	2,102	7,323	0.26
α	5.57	1.67	9.97	0.49
β	1.43E-04	9.55E-05	1.85E-04	0.16
ϕ	0.47	-0.22	0.98	0.80
σ_R	0.46	0.32	0.67	0.20
T_a	0.33	0.05	0.62	0.46
P_a	3.72	0.77	7.12	0.43
S_{MSR}	6,996	5,159	9,932	0.20
S_{EQ}	12,511	7,261	17,999	0.21
S_{MSY}	4,626	3,158	6,349	0.17

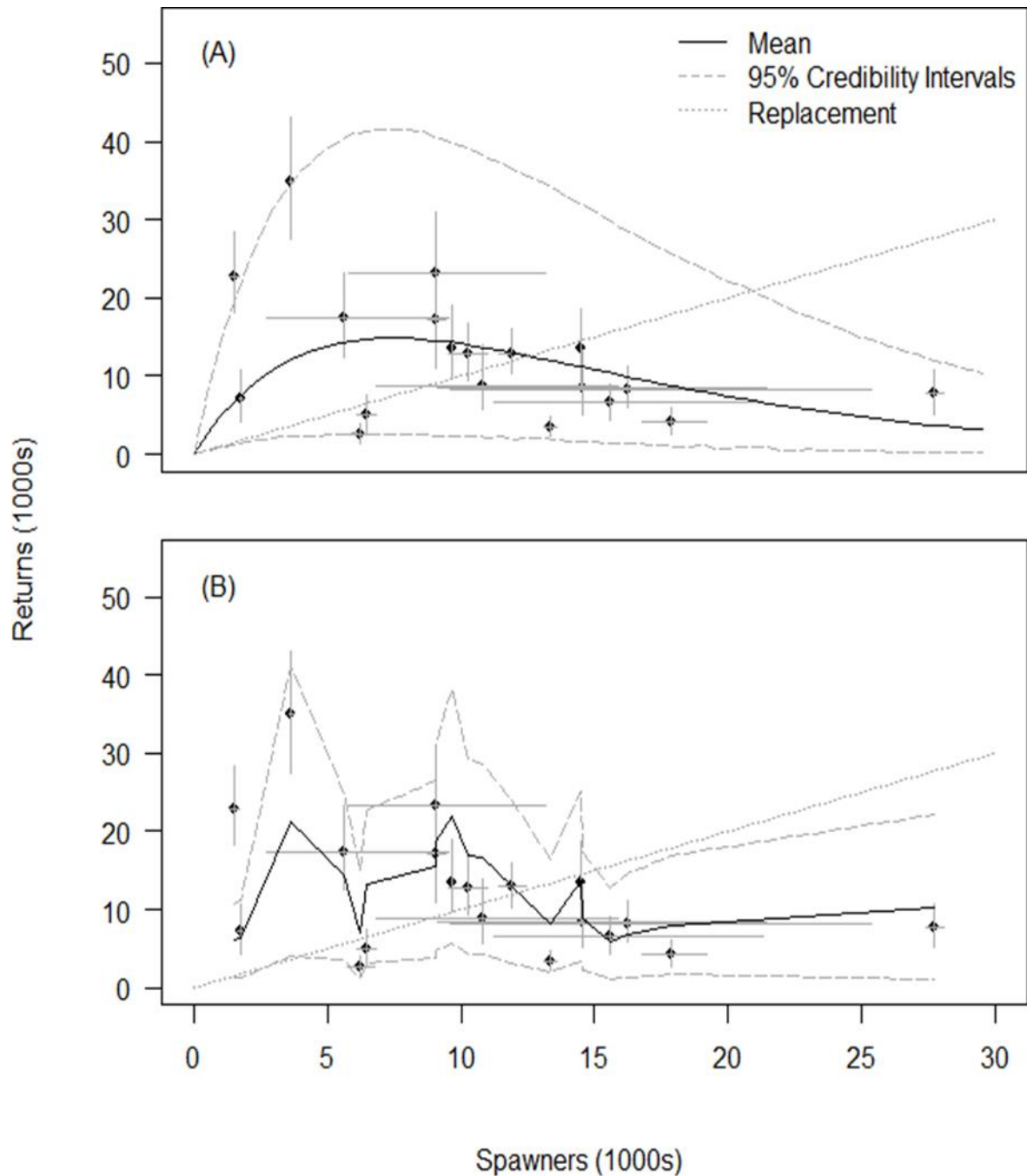


Figure 1. Base Ricker modeled spawner-recruit relationship (A) and an environmental covariate parameterizations considering the effects of maximum fall temperature and precipitation anomalies for Kwethluk River Chinook Salmon, brood years 1992–2010. Error bars on points represent the 95% Bayesian credibility intervals on brood year linked escapement and recruitment and long dashed gray curves are 95% Bayesian credibility intervals for predicted recruitment given stock size. The dashed line represents 1:1 replacement.

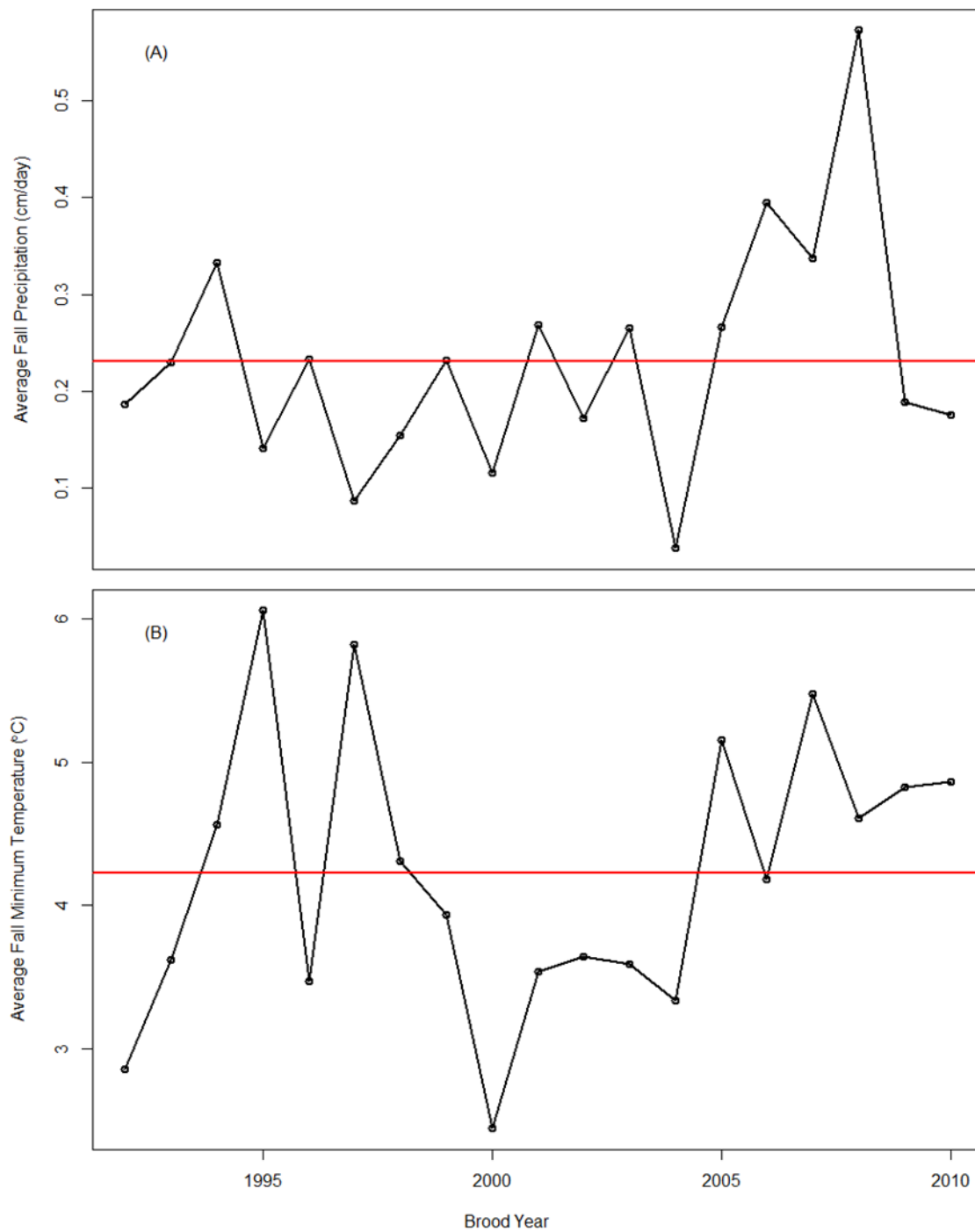


Figure 2. Annual fall average precipitation (cm/day; A) and minimum temperatures (°C; B), calculated from bethel, airport data (NCDC 2017; 1992-2010). Red horizontal lines indicate the 19 year (1992-2010) averages. Temperature and precipitation anomalies were calculated, as the difference in daily norms and the 19 year average.

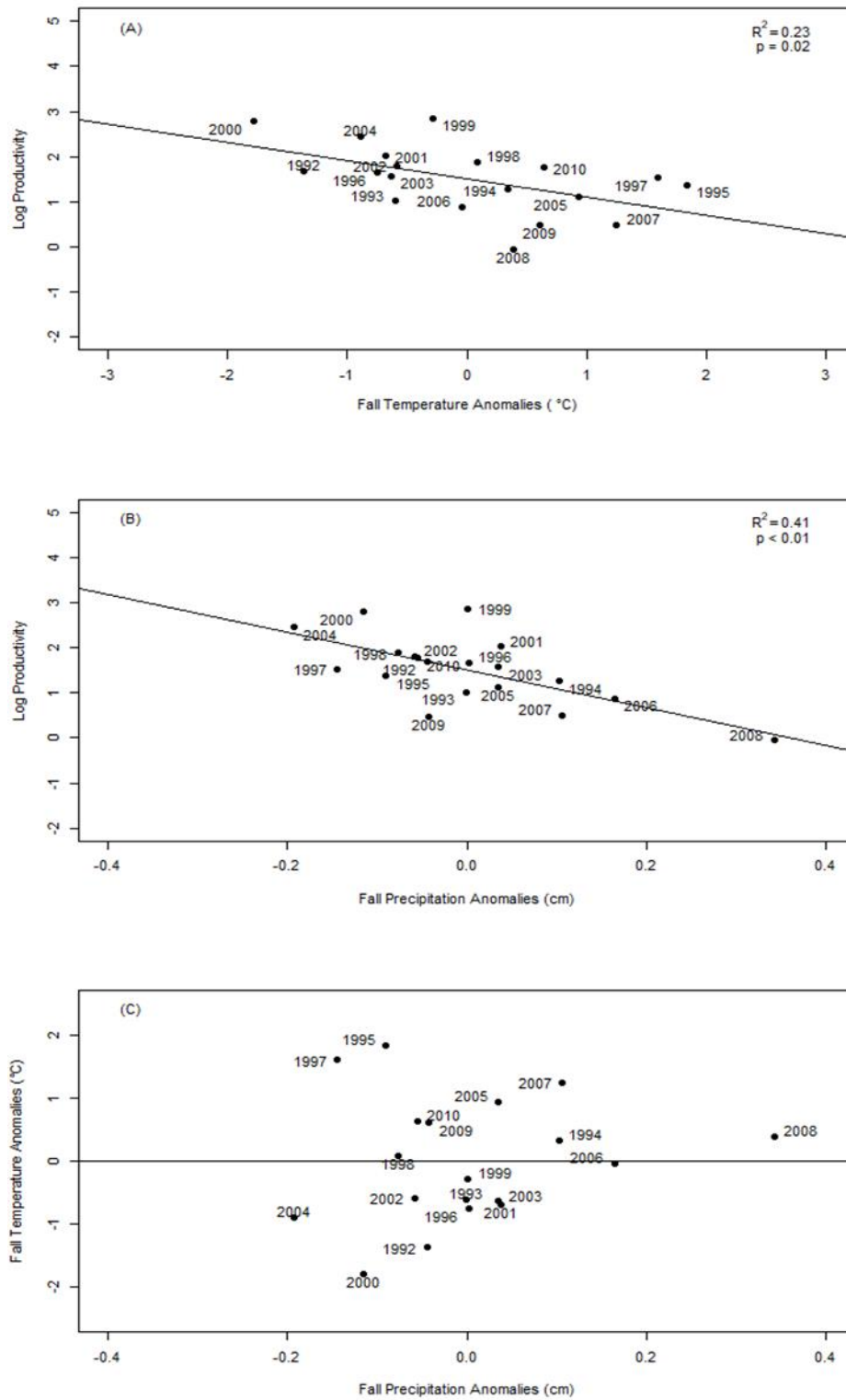


Figure 2. The relationship between the base Ricker estimates of log productivity and Fall temperature (A) and precipitation (B) anomalies and between predictive variables (C).

Appendix A.—RJAGS model code for a base Ricker spawner recruit model of Kewthluk River Chinook Salmon, 1992–2017.

```
#####
# AR[1] STOCK-RECRUITMENT Base model specification#####
#####
#data are log normally distributed run reconstruction estimates
data{
  for(y in 1:Y) {
    S_sigma[y] <- sqrt(log(pow(S_CV[y],2)+1))
    S_tau[y] <- 1/pow(S_sigma[y],2)
    R_sigma[y] <- sqrt(log(pow(R_CV[y],2)+1))
    R_tau[y] <- 1/pow(R_sigma[y],2)
    log_est_R[y] <-log(est_R[y])
    log_est_S[y] <-log(est_S[y])
    S.temp[y] ~ dlnorm(log_est_S[y],S_tau[y])
    R.temp[y] ~ dlnorm(log_est_R[y],R_tau[y])
    Ln.R[y] <-log(R.temp[y])
    S[y] <- S.temp[y]
  }
}
model{
# priors
Ln.alpha ~ dnorm(0,1.0E-6)l(0,5)
beta ~ dunif(1.0E-4,1)
phi ~ dnorm(0,1.0E-6)l(-1,1)
R.tau ~ dgamma(0.01,0.01)
R0.tau <- R.tau*(1-phi*phi)
Ln.resid.0 ~ dnorm(0,R0.tau)

# likelihood
for(y in 1:Y) {
  Ln.R[y] ~ dt(Ln.R.mu[y], R.tau,500)
  R[y]<-exp(Ln.R[y])
  Temp.Ln.R.mu[y] <- log(S[y])+Ln.alpha-beta*S[y] # Ricker 1954
  Ln.resid[y]<- log(R[y])-Temp.Ln.R.mu[y]
  resid[y]<- exp(Ln.resid[y])
  Ln.alpha.y[y]<-Ln.resid[y]+Ln.alpha
  alpha.y[y]<- exp(Ln.alpha.y[y])
}
Ln.R.mu[1] <- Temp.Ln.R.mu[1]+phi*Ln.resid.0
for(y in 2:Y) {
  Ln.R.mu[y]<-Temp.Ln.R.mu[y]+phi*Ln.resid[y-1]
}
# Predicted R given S:
for (y in 1:length(S2)) {
  R.Pred[y] <- min(S2[y] * exp(Ln.alpha.cor - beta * S2[y]),1.0E6)
}
}"
```


Appendix B.—RJAGS model code for a Ricker spawner recruit model with temperature and precipitation effects
Kewthluk River Chinook Salmon, 1992–2017.

```
#####
# STOCK-RECRUITMENT model W/Temperature and precipitation effects
#####
#data are log normally distributed run reconstruction estimates
"
data{
  for(y in 1:Y) {
    S_sigma[y] <- sqrt(log(pow(S_CV[y],2)+1))
    S_tau[y] <- 1/pow(S_sigma[y],2)
    R_sigma[y] <- sqrt(log(pow(R_CV[y],2)+1))
    R_tau[y] <- 1/pow(R_sigma[y],2)
    log_est_R[y] <-log(est_R[y])
    log_est_S[y] <-log(est_S[y])
    S.temp[y] ~ dlnorm(log_est_S[y],S_tau[y])
    R.temp[y] ~ dlnorm(log_est_R[y],R_tau[y])
    Ln.R[y] <-log(R.temp[y])
    S[y] <- S.temp[y]
  }
}
model{
  # priors
  Ln.alpha ~ dnorm(0,1.0E-6)l(0,5)
  beta ~ dnorm(0,1.0E-6)l(0,)
  phi ~ dnorm(0,1.0E-6)l(-1,1)
  R.tau ~ dgamma(0.01,0.01)
  R0.tau <- R.tau*(1-phi*phi)
  Ln.resid.0 ~ dnorm(0,R0.tau)
  gamma ~ dnorm(0,1.0E-6)
  lamda ~ dnorm(0,1.0E-6)

  # likelihood
  for(y in 1:Y) {
    Ln.R.mu[y] ~ dt(Ln.R.mu[y], R.tau,500)
    R[y]<-exp(Ln.R[y])
    Temp.Ln.R.mu[y] <- log(S[y])+Ln.alpha-((beta*S[y])+(gamma*temp[y])+(lamda*precip[y])) # Ricker 1954
    Ln.resid[y]<- log(R[y])-Temp.Ln.R.mu[y]
    resid[y]<- exp(Ln.resid[y])
    Ln.alpha.y[y]<-Ln.resid[y]+Ln.alpha
    alpha.y[y]<- exp(Ln.alpha.y[y])
  }
  Ln.R.mu[1] <- Temp.Ln.R.mu[1]+phi*Ln.resid.0
  for(y in 2:Y) {
    Ln.R.mu[y]<-Temp.Ln.R.mu[y]+phi*Ln.resid[y-1]
  }
  # Predicted R given S:
  for (y in 1:length(S)) {
    Ln.R.Pred[y] <- log(S[y])+Ln.alpha-((beta*S[y])+(gamma*temp[y])+(lamda*precip[y]))
    R.Pred[y] <- exp(Ln.R.Pred[y])
    RPS[y]<- R.Pred[y]/S[y]
  }
}"
```

PRESS RELEASE

Recent declines in the productivity and abundance of Chinook Salmon stocks throughout the Arctic-Yukon-Kuskokwim (AYK) region have resulted in restrictions to commercial and subsistence fisheries. These restrictions have highlighted a need for greater clarity into the dynamics that regulate these populations. We evaluated the role that freshwater environmental and density dependent factors have on Chinook Salmon returns to the Kwethluk River. We found a population-level response to spawning abundances and environmental variation during the fall of the brood year. Above average brood year fall temperatures and precipitation negatively affect productivity, indicating that spawning abundance and above optimal temperatures and flooding during the early life stages are important factors driving the productivity of Chinook Salmon in the Kwethluk River.

PROJECT EVALUATION

The proposed project had two primary objectives as follows:

Objective 1: *Identify the relationship between smolt abundance and spawning escapements. And compare variations in adult recruitment with patterns of smolt production to partition density dependent effects between freshwater and other phases of the life cycle.* We completed this objective as originally planned. We report on our findings related to this objective in the attached draft manuscript(s).

Objective 2: *Identify environmental variables that may be related to changes in freshwater habitat resulting in variations in mortality.* We completed this objective as originally planned. We report on our findings related to this objective in the attached manuscript(s).

DELIVERABLES

The findings of this project have been and will continue to be distributed through conference and management meeting presentations, agency reports and or peer-reviewed manuscript(s). We have completed 3 presentations, and intend to submit versions of the attached manuscripts for publication, as agency reports and or peer-reviewed manuscripts, by the summer of 2019.

Reports:

Semiannual progress reports June and December 2017, and June 2018.

Presentations:

Harper, K.C., J.K. Boersma, and L.G. Coggins. Monitoring Chinook Salmon smolt in Western AK to evaluate freshwater density dependency. Western division of the American fisheries Society Conference. Anchorage Alaska.

Harper, K.C., J.K. Boersma, and L.G. Coggins. Monitoring Chinook Salmon smolt in Western AK to evaluate freshwater density dependency. Alaska Chapter of the American fisheries Society Conference. Fairbanks Alaska.

Meetings Participated:

2016, 2017, 2018 Kuskokwim River Interagency Meetings.
Regional advisory council meetings March 2017 and 2018.

PROJECT DATA SUMMARY

Summary data and all model code for each analysis are attached as appendices to this report. All model outputs and un-summarized data are available upon request from the PI.

