Final Report for Pacific Salmon Commission Northern Endowment Funds

Atnarko River Chinook Salmon Spawning Escapement Estimation for 2018

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1 INTRODUCTION

1.1 Background

Approximately a decade ago, the Coded Wire Tag (CWT) Pacific Salmon Commission (PSC) Working Group identified that Central British Columbia (BC) was a major production region of Chinook salmon without an indicator stock (PSC Coded Wire Tag Workgroup 2008). Starting in 2009, a plan was implemented to convert Atnarko Chinook into an exploitation rate indicator for Pacific Salmon Commission assessments (Vélez-Espino *et al.* 2010). This required a mark-recapture program, the application of more Coded Wire Tags (CTWs) to Atnarko Chinook hatchery releases (under separate submission to the Northern Endowment Funds), and sampling of First Nation, sport, and terminal fisheries. Once five years of rigorous mark-recaptures were complete, Vélez-Espino *et al.* (2014) were able to calibrate historical data on the stock back to 1990. In 2012, Atnarko Chinook were added as an exploitation rate indicator in PSC exploitation rate assessments (Pacific Salmon Commission 2012).

The Atnarko River is one of two exploitation rate indicator stocks for North Coast BC and is the only Chinook rate indicator on the mainland of BC between Kitsumkalum River and Harrison River. The Atnarko River and Kitsumkalum River stocks fall into different Conservation Units and the Central Coast population is not well represented by Kitsumkalum as they differ in genetics, life history and ecology (Holtby and Ciruna 2007; Vélez-Espino *et al.* 2011). Specifically, Atnarko Chinook are predominantly ocean-type (Pestal 2004), while Kitsumkalum Chinook are mostly stream-type (McNicol 1999). In addition, current and historic fishing mortality of Atnarko and Kitsumkalum Chinook occur in different proportions within Canadian Aggregate Abundance Based Management (AABM) fisheries, US AABM fisheries, and Individual Stock Based Management (ISBM) terminal fisheries (Pacific Salmon Commission Chinook Technical Committee 2018a).

A majority of Chinook entering the Bella Coola River spawn in the Atnarko River and the Atnarko River Chinook stock is the largest contributor to the Bella Coola-Dean Conservation Unit. Similarly timed summer-run stocks in the Central Coast include the Chuckwalla River and Owikeno Lake tributary stocks in Rivers Inlet, as well as the Dean River. Although Chuckwalla River Chinook are no longer enhanced, historical hatchery marked releases from the Chuckwalla River showed tag recoveries in similar fisheries to Atnarko River recoveries.

1.2 The Atnarko River

The Atnarko River feeds the Bella Coola River and is situated in Statistical Area 8 on the Central Coast of B.C. (Figure 1). The river is north of Cape Caution and resides within the Northern Fund region of the Pacific Salmon Treaty. The Atnarko River drains a 2,440 km^2 watershed and merges with the Talchako River approximately 45 km downstream from Knot Lake to form the Bella Coola River (Figure 2). With the exception of Charlotte Lake and the headwaters of the Hotnarko River, the Atnarko and its tributaries are situated within the boundaries of Tweedsmuir Provincial Park.

The Atnarko River can be divided into three segments with biotic and abiotic attributes specific to Chinook salmon. Atnarko Chinook salmon are primarily distributed between Hotnarko River and Janet Creek in the upper Atnarko River, and from Alger Creek to the confluence of the Talchako River in the lower Atnarko River (Figure 2; Vélez-Espino *et al.* 2010). The upper Atnarko River has many sections with deep and large holding areas that constitute high quality spawning areas. Overall, the spawning habitat is excellent in the upper section with exception to the lower part where the river gradient decreases and water velocity slows. The middle segment is characterized by sections with larger substrate, boulders, and increased gradient drops. The higher water velocity creates a lower quality spawning habitat. Chinook salmon holding capacity in this section is limited and spawning is spread-out. The Lower segment is characterized by braided sections and is predominantly high-quality Chinook spawning habitat in its middle and lower portions. The upper part of the Lower section does have some areas with large boulders and large substrate (due to increases in the river gradient), and thus limited areas to spawn. Most of the holding areas are small to moderately sized, with the exception of Alger's Pool (the largest holding area on the river). These holding areas have suitable spawning habitat located both above and below.

Atnarko Chinook salmon are easily captured and recovered as the system is not as susceptible to fall flooding as many other coastal Chinook systems (BCWCS 2007). The past years of experience working on the system and close proximity of qualified personnel also reduce the risks associated with conducting mark-recapture programs on remote systems. Given past mark-recapture and dead pitch programs conducted on the Atnarko River, a good understanding of effort requirements for sufficient tag application as well as carcass recovery exists.

1.3 Objectives

The primary objective of the 2018 Atnarko River Chinook Escapement Estimation Project was to generate an unbiased total spawning escapement estimate of Atnarko River Chinook salmon (*Onchorynchus tshawytscha*) with a PSC data standard coefficient of variation (CV) of 15% or less. The project has continued to meet this standard every year since 2009 (Table 1). Additional objectives include estimating the number of large wild Chinook returning, age structure of the population (within 5% of the true value), and Proportion of Natural Influence (PNI; conducted by SEP separately).

2 METHODS

2.1 In Field Methods

All in-field operations were completed following the Operational Guideline (Winther and Krimmer 2018). Updates are added annually prior to the field program to improve operations. Field operations are summarized below.

2.1.1 Marking

Chinook were tagged on the Atnarko River from August 16th 2018 to September 7th 2018. During this period, 1462 tags were applied and the tagging goal of 1,000 Chinook was achieved. Each Chinook was tagged twice. Every fish received an individually numbered metal #3 Kurl-Lock tag (http://www.ketchum.ca/) that was carefully crimped and a secondary mark consisting of a hole punched through the operculum. This allowed fish with missing Kurl-Lock tags to be included in escapement estimates. The number of punches a fish received was determined by which river section the fish was tagged in. Activity, recorder’s initials, net type, reach number, sex, punch scheme, tag number, adipose presence, and state (live/dead) was recorded for every fish tagged or re-encountered.

For the purpose of this field program, the Atnarko River is divided into three sections (Upper, Middle, and Lower) and each section is further divided into two reaches (Upper: Reach 1 to 2, Middle: Reach 3 to 4, Lower:

Reach 5 to 6; Figure 3). These divisions are based on accessibility to the river, historical evidence of spawning similarity, and ability to drift each reach in a single day. Tagging occurred along all reaches by multiple crews every day. Chinook tagged in the Upper section (Reach 1 to 2) received one punch applied to the right side, those tagged in the Middle section (Reach 3 to 4) received two punches applied to the left side and those tagged in the Lower section (Reach 5 to 6) received one punch on the left side.

Chinook were captured using both gill nets and seine nets. Gill nets were used in all reaches of the river, whereas seine nets could only be used in a few spots located in Reach 2 and Reach 5 due to river morphology. For a majority of the experiment, multiple crews were present on the river tagging in different reaches each day.

Effort was made to apply tags to reflect perceived fish distribution based on crew observations and previous hatchery release sites. In the past, these portions were 40% in the Upper Reaches, 20% in the Middle Reaches, and 40% in the Lower Reaches based on historical observations. In 2018, 50.55% were tagged in the Upper Reaches, 9.10% were tagged in the Middle Reaches, and 40.36% were tagged in the Lower Reaches. Multiple tagging locations within each reach were chosen to improve marked fish mixing completely with the unmarked population.

Effort was made to apply tags to as many Chinook as possible, regardless of sex. Disparity between portion of tagged reflects selective bias caused by using gill nets, which are used for a majority of the tagging days, and removal of females for broodstock collection. Of the total tagged fish, 17.24% were females, 81.67% were males, and 1.09% were jacks.

Tagging continued exclusively until August 27th 2018. For the final 11 days of tagging, broodstock collection simultaneously occurred.

2.1.2 Broodstock collection

Broodstock collection occurred between August 28th 2018 and September 21st 2018. Broodstock included both in-field gamete collection and transporting unripe Chinook to the hatchery for holding until there were ready to spawn. When tagging and broodstock occurred simultaneously, fish that were appropriate for broodstock were removed and those that were not suitable for broodstock were tagged and released. All Chinook encounters, releases, and removals were recorded and a total of 1,075 Chinook salmon were removed from the Atnarko River for broodstock. Of the 1,075 fish removed, 153 Chinook were tagged, thus leaving a total of 1,209 tagged Chinook (207 females, 1,086 males, and 16 jacks) in the population available for dead-pitch recovery.

In 2018, broodstock targeted Chinook without adipose clipped fins (ACF), this will be considered when calculating wild and hatchery contributions to escapement.

2.1.3 Carcass recovery

Dead-pitch began on September 18th 2018 when multiple carcasses were discovered during broodstock activities and continued until October 4th 2018. Carcasses discovered during other activities prior to September 19th 2018 were recorded. A total of 1,395 carcasses were recovered consisting of 44.66% females, 55.20% male, and 0.14% jack carcasses with a majority of recoveries occurring in the Lower Reaches.

Dead-pitch crews consisted of two swimmer/divers, one oarsman and one recorder at minimum. Divers were equipped with a gaff hook and shore crews were equipped with fish pews. Carcasses were recovered throughout all six river reaches.

All carcasses recovered were checked for pre-spawn mortality/egg retention, sex, tag number, punch scheme, and ACF fins (indicating a fish of hatchery origin and probably a CWT). Recovery reach was also recorded along with the recorder's initials. Once recorded, carcasses were pitched high onto the banks so they would not be counted again. Heads from all ACF Chinook spotted during dead-pitch were removed, and sent for CWT dissection at to J.O. Thomas and Associates. In 2018, 214 heads were collected.

2.1.4 Biological Sampling

Scale samples and nose-fork (NF) lengths were taken from 516 non-ACF Chinook during tagging for ageing analysis. Scale samples, NF lengths, and post-orbital-hyperal (POH) lengths were taken from 545 non-ACF Chinook during dead-pitch. Scales were placed in a labelled waterproof envelope and five scales were mounted into corresponding scalebooks for each fish at the end of the program. Additionally, a total of 123 scale samples were collected from ACF (CWT) Chinook were sampled. These scales were compared to their respective CWT ages to determine error in scale readings.

Scale samples were taken to represent stream reaches. All scale samples were shipped to the Fish Ageing Laboratory at the Pacific Biological Station for reading using the Gilbert and Rich (1927) method. Only scale samples that produce both marine and freshwater ages following were reported and used to determine portions of spawning escapement estimates for each age.

The POH and NF lengths taken from carcasses during dead-pitch were used to derive a linear equation to predict the POH length of fish encountered during tagging using the NF length that was recorded. This was done to reduce live fish handling time during tagging. All males with measured or calculated POH lengths smaller than 460 mm were recorded as jacks.

2.1.5 Encounter Histories

Encounter histories were created following methods described in Vélez-Espino *et al.* (2010) and Vélez-Espino *et al* (2016; Table 2). In 2018, a total of 3,756 Individual Encounter Histories (IEH) were used in the analyses. Encounters were broken into 11 time periods consisting of 3 or 4 days that similar events were occurring (e.g. mark application, broodstock collection, dead-pitch, etc.). There were 48 instances were tags were either unreadable, the tag number was not read, or the tag was missing. These fish were identified as tagged by their punch scheme (secondary mark) and this information was used to randomly assign a tag number of any tag available for recapture respecting the same sex, time tagged, ACF/non-ACF, and tagged location (punch scheme) as in Vélez-Espino *et al.* (2010).

2.2 Analyses

2.2.1 Petersen Estimate

Spawning escapement was estimated using the Chapman modification of the Petersen estimator (Ricker 1975) stratifying by sex.

$$N = \frac{(C_{i,r}+1)(M_{i,r}+1)}{(R_{i,r}+1)}$$

$$Variance\ of\ N = \frac{(M+1)^2(C+1)(C-R)}{(R+1)^2(R+2)} = \frac{N^2(C-R)}{(C+1)(R+2)}$$

$$\text{Standard error} = \sqrt{\text{Variance of } N},$$

$$\text{95\% confidence limits} = \text{N} \pm t(\text{Standard error})$$

Where *N* is the population estimate, *C* is the total number of fish recovered, *M* is the total number of fish tagged (with all tagged broodstock removed), and *R* is the number of tagged fish recovered with primary or secondary marking. Population estimates are completed separately for each sex and summed together for an estimate of the total population to reduce bias. The number of marked fish used in the Petersen method was adjusted to account for the tagged fish removed during broodstock. The Petersen relies on the following assumptions to be true:

1. All Chinook suffer the same mortality rates
2. All Chinook have an equal probability of capture (application) and recapture (carcass recovery)
3. Chinook do not lose their marks, all marks are recognizable and reported upon encounter
4. Marked Chinook mix randomly with unmarked Chinook between marking and recovery
5. There is no immigration or emigration between marking and recovery (closed population)

Assumption's 1, 2, and 5 are often violated to some degree in mark-recapture experiments on salmonids (Vélez-Espino *et al.* (2016), thus it is best to rely on escapement estimates that can consider open populations, temporal variation in survival rates, and heterogenic capture probabilities by utilizing IEH data for analyses (Vélez-Espino *et al.* 2010). The Petersen estimate is reported during post-season discussions on Atnarko River Chinook as a preliminary estimate until the best model escapement estimate is available.

2.2.2 Size, and mortality related bias

Size and mortality bias testing was completed using R 3.5.2. Kolmogorov-Smirnov two sample tests (Sokal and Rohlf 1981) were used to compare POH length frequency distributions testing for size bias between tagged and recovery samples and recovered tags and unrecovered tags within males and females. Length frequency distributions were not compared between tagged and untagged recovery groups due to small sample size (e.g. only 4 tagged females with POH measurements during carcass recovery).Additionally, jacks were recovered at too low numbers to make comparisons.

Mark application bias was assessed by comparing occurrence of pre-spawn mortality (egg retention of 70% or more), between marked and unmarked females recovered during dead-pitch using a Fisher exact test as the assumptions of a chi-square contingency table would be violated (Zar 1985).

Bias in sex was not assessed as strata were not pooled during analysis. Temporal bias was not assessed as it is incorporated directly into the analysis described below.

2.2.3 Closure test

The closure test for time-specific data developed by Stanley and Burnham (1999) was used to test the null hypothesis of closed-population model M_t against the open population Jolly-Seber model using a chi-square test as in Vélez-Espino *et al.* (2010) using the computer software Close Test Version 3 (T.R. Stanley and J.D. Richards, USGS, Fort Collins Center, Colorado)

2.2.4 Model Framework and open-population models

Escapement estimates were derived by the methods of Vélez-Espino *et al.* (2010) following the approach in Lebreton *et al.* (1992):

1. Start from a global model compatible with species biology and asses its fit using goodness-of-fit tests
2. Select a more parsimonious model using Akaike's Information Criterion (AIC) to limit the number of formal tests
3. Compare parsimonious model with neighbouring models using likelihood ratio tests (LRT)
4. Obtain maximum likelihood estimates of model parameters and their estimates of precision

As in Vélez-Espino *et al.* (2010), the Jolly-Seber model using multinomial distribution from the total population was applied to data in 9 open-population models using POPAN models in program MARK (http://www.phidot.org/software/mark/). Each model was defined by its assumptions about the probability of capture, survival, and recruitment of the likelihood estimator using recapture information. Data was stratified by sex and time to avoid bias. The evaluation of closed-population models was not necessary in 2018 due to the results of the closure tests (Table 3). If the null hypothesis of the test was not rejected, the evaluation of closed-population models would have been conducted separately for maximum likelihood estimators as demonstrated by Vélez-Espino *et al.* (2010) following Otis *et al.* (1978) and Chao (2001). AIC-based model selection was conducted using MARK. Once the best model was selected, model parameters and their estimates of precision were obtained. These parameters were then used in the modified Jolly-Seber developed by Schwarz *et al.* (1993) to determine both net (those that survive to spawn) and gross population (total individuals) estimates for each strata (males, females, jack) in MARK.

Pre-spawning mortality was also calculated using the ratio of net-to-gross escapement as in Velez-Espino *et al*. (2016).

2.2.5 Wild and Hatchery contribution

Atnarko River Chinook hatchery production occurs at Snootli Creek Hatchery were around 2 million fry are released annually with 400,000 of those receiving ACF and CWTs. All heads from ACF carcasses were collected during carcass recovery for CWT reading. Estimates of the contribution of hatchery-reared Chinook to the total escapement were calculated by expanding the percentage of CWT's in escapement counts by tag code segregated by strata (male, female jack) including accounting for 'no pin' recoveries, following the methods described in Vélez-Espino *et al.* (2010).

Due to broodstock targeting non-ACF fish, only mark rate from dead-pitch was used in the 2018 hatchery contribution calculation. After hatchery contribution is determined for each strata (female, male, jack), a total large wild population estimate will also be calculated.

2.2.6 Age Distribution

An estimate of age composition will be made from the results of scale and CTW ageing analysis.

3 RESULTS

3.1 Petersen Estimate

Of the 1,395 carcasses recovered, 112 were identified as tagged by Kurl-Lock or punch scheme. The Petersen method estimated the Atnarko Chinook population to consist of 6,490 (95% CI: 4,230 to 9,867) females, 8,916 (95% CI: 7,293 to 10,896) males, and 51 (95% CI: 10 to 53) jacks for a total spawning escapement of 15,456 fish (95% CI: 12,184 to 18,728). The coefficient of variation was 21.47%, 9.61%, and 57.74% for females, males and jacks respectively, and 10.59% for the combined population. This estimate does not include fish removed from the system for broodstock.

3.2 Size and Mortality Bias

No significant differences were found for either male or female Chinook salmon when comparing POH length frequency distributions between tagged and recovered fish (KS two sample t-test: p>0.05, and recovered and unrecovered tagged fish (KS two sample t-tests: p>0.05). These results suggest that the tag application and recovery process was not size selective. Mean POH of female Chinook salmon sampled was 711 mm and 607mm for males with standard deviations of 45 mm and 78 mm respectively.

Out of all 17 tagged female carcasses inspected, one female exhibited egg retention, and 4 females out of all 513 untagged female carcasses inspected exhibited egg retention. Bias caused from mark application was not detected when comparing pre-spawn mortality between tagged and untagged females (Fisher exact: p=0.151).

3.3 Tag loss

Tag retention for Kurl-Lock tags was estimated to be 7.14% as 8 of 112 carcasses recovered had lost their Kurl-Lock tag but were all still identified as tagged by their punch scheme. This was lower than encountered in other years of the experiment.

3.4 Closure test

Closure tests indicated there were both additions and losses from the population (Table 3).

3.5 Open-population models and closed-population models

Open-population models are defined by the probability of capture (*p*), the probability of survival (*s*), and the probability of recruitment (i.e., entering the system) (*b*) under time-specific (*t*), group-specific (*g*), time- and group-specific (*g**t*), and/or invariant (*) conditions. Models including time variant capture probabilities *p*(*t*) or *p*(*g**t*) were not included in the list because they have unidentifiable parameters that generate unreasonable parameter values (Amstrup *et al.* 2005). Based on the AIC weights, the best model corresponded to {*p*(*g*), *s*(g,t), *b*(*g**t*)}, which indicates differences in capture probabilities between groups, time-invariant survival probabilities and both time-specific and group-specific differences in entry probabilities.

The Best model selected estimated the Atnarko River Chinook escapement to be 5,181 (95% CI: 3,993 to 6723) females, 7,593 (95% CI: 6,541 to 8,815) males, and 234 (95% CI: 66 to 2824) jacks for a total spawning escapement of 13, 008 (95% CI: 10,599 to 18,362) Chinook (Figure 4; Table 1). The coefficient of variation was 13.4%, 7.6%, and 198.3% for females, males and jacks respectively, and 7.8% for the entire population (Table 1). Additionally, 2018 data supports the current correlation between number of IEHs, and the best model escapement estimate (Figure 5).

Pre-spawning mortality (which is confounded with permanent emigration; see Velez-Espino *et al*. 2016) was calculated from the ratio of female net-to-gross escapement as 6.7%.

3.6 Age distribution

Scale samples were collected from non-ACF 1,061 (422 female, 632 male, and 7 jack) Chinook in 2018. Of all scale samples collected, 661 samples were read successfully, 276 were partially read, and 124 were unreadable. Of the 661 successfully read, 31.92% were age-3, 42.21% were age-4, 23.15% were age-5, and 2.72% were age-6. Freshwater annulus revealed that 78.06% Chinook were ocean-type and 21.94% were stream-type. At the age-specific level: 99.05% of the age-3 fish, 78.14% of the age-4 fish, 56.86% of the age-5 fish and 11.11% of the age-6 fish exhibited ocean-type life history.

3.7 Wild and Hatchery Contribution

Hatchery contribution was 58.3% and 5,328 Large Wild Atnarko Chinook Salmon were estimated to contribute to escapement in 2018 (Table 1; Figure 4).

4 DISCUSSION

We met our objectives by generating an unbiased total spawning escapement estimate of Atnarko River Chinook salmon (*Onchorynchus tshawytscha*) within a PSC data standard coefficient of variation (CV) of 15% by applying modern analytical techniques (Table 1; Figure 4). The stratified Petersen method over-estimated escapement relative to the best model escapement estimate by 18.8%. These results are similar to those found by Vélez-Espino *et al*. (2016), who found that the Petersen method tends to over-estimate escapement. Additionally, the data did not meet the closed-population assumption, and the best model parameters indicated there were differences in capture probabilities between groups, time-variant survival probabilities and both time-specific and group-specific differences in entry probabilities. Thus Atnarko Chinook escapement data continues to support the application of a more robust technique to determine escapement as a more accurate and precise method to estimate escapement (Vélez-Espino *et al*. 2010; Vélez-Espino *et al*. 2016).

Annual robust spawning escapement estimates and sampling efforts for Atnarko River Chinook allows Fisheries and Oceans Canada to meet current Pacific Salmon Treaty obligations. Specifically, a rigorous escapement and sampling program is required to meet requirements to determine escapement in relation to current escapement goals, identify exploitation rates, monitor trends in stock status, and support sustainable harvest. An agency accepted habitat-based estimate of S_{MSY} (Parken *et al.* 2006; Velez-Espino *et al.* 2014) has already been derived for the Atnarko River and adopted under the newly signed Pacific Salmon Treaty. The 2018 large wild Chinook population estimate was above the current escapement goal of 5,009 wild Chinook as with previous years, with exception to 1997 and 2012 (Figure 4; Pacific Salmon Commission Chinook

Technical Committee 2018b; Velez-Espino *et al.* 2014). DFO Biologists will be conducting a Stock-Recruitment analysis to refine the current escapement goal starting in 2019; this work will further improve the quality of Atnarko River Chinook stock status assessments. Additionally, PSC Chinook Technical Committee members have been working to include Atnarko River Chinook as a Central British Columbia Model stock in the PSC Chinook Model for model calibration and forecasting as the Kitsumkalum is currently the only CWT North/Central BC Model stock. Further work using robust escapement estimates to spawning grounds is needed to test the performance of the split between the North/Central BC Model stocks into two stocks prior to its official inclusion in the model. A mark-recapture program is planned for the Atnarko River Chinook in 2019 to continue to fulfill the above mentioned obligations and support research which will enlighten our knowledge of the Chinook stock and support the application of science-based harvest management strategies.

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FIGURES

Figure 1. Map of British Columbia showing location of the Atnarko River.

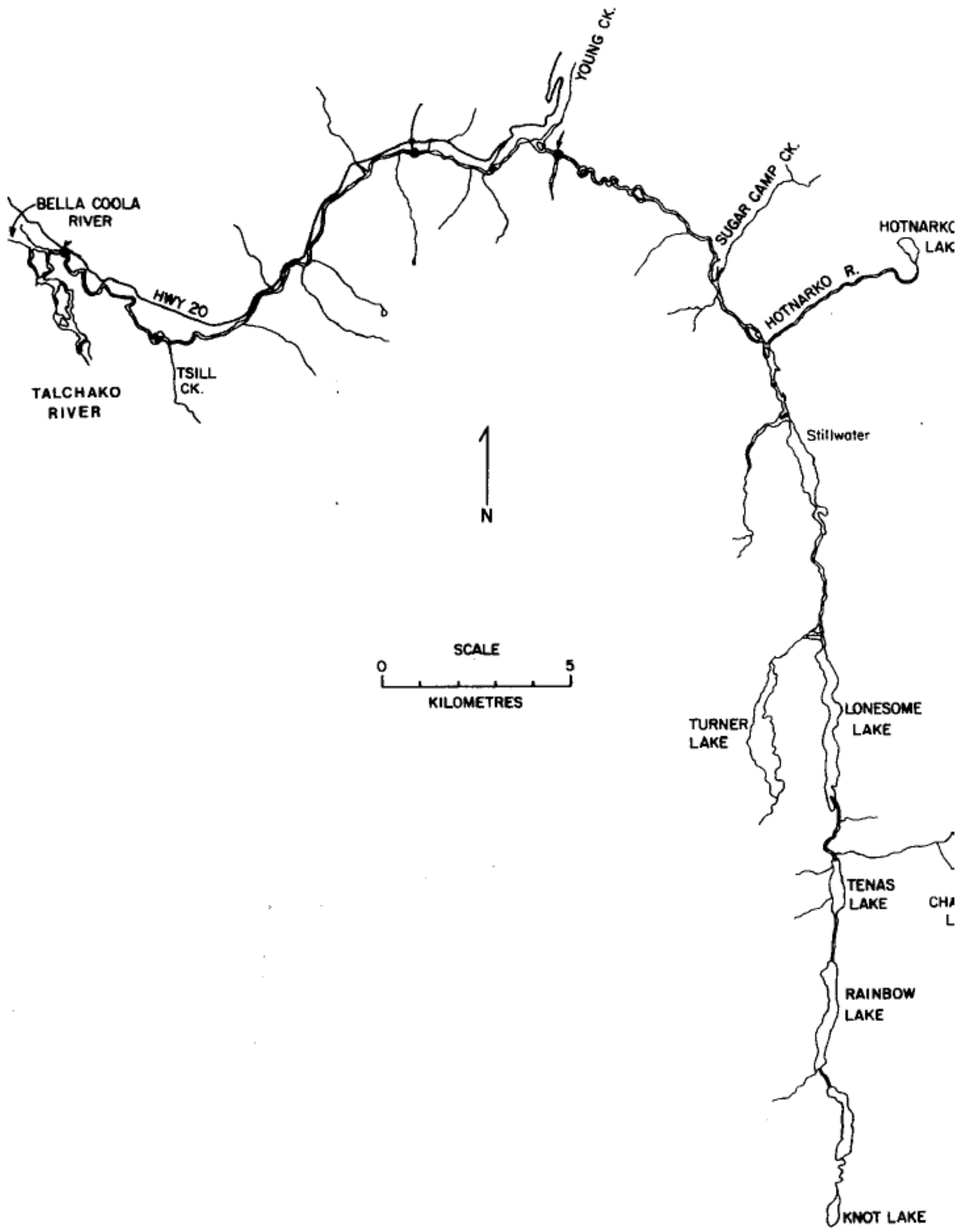

Figure 2. The Atnarko River drainage.

Figure 3. Atnarko River project sample area.

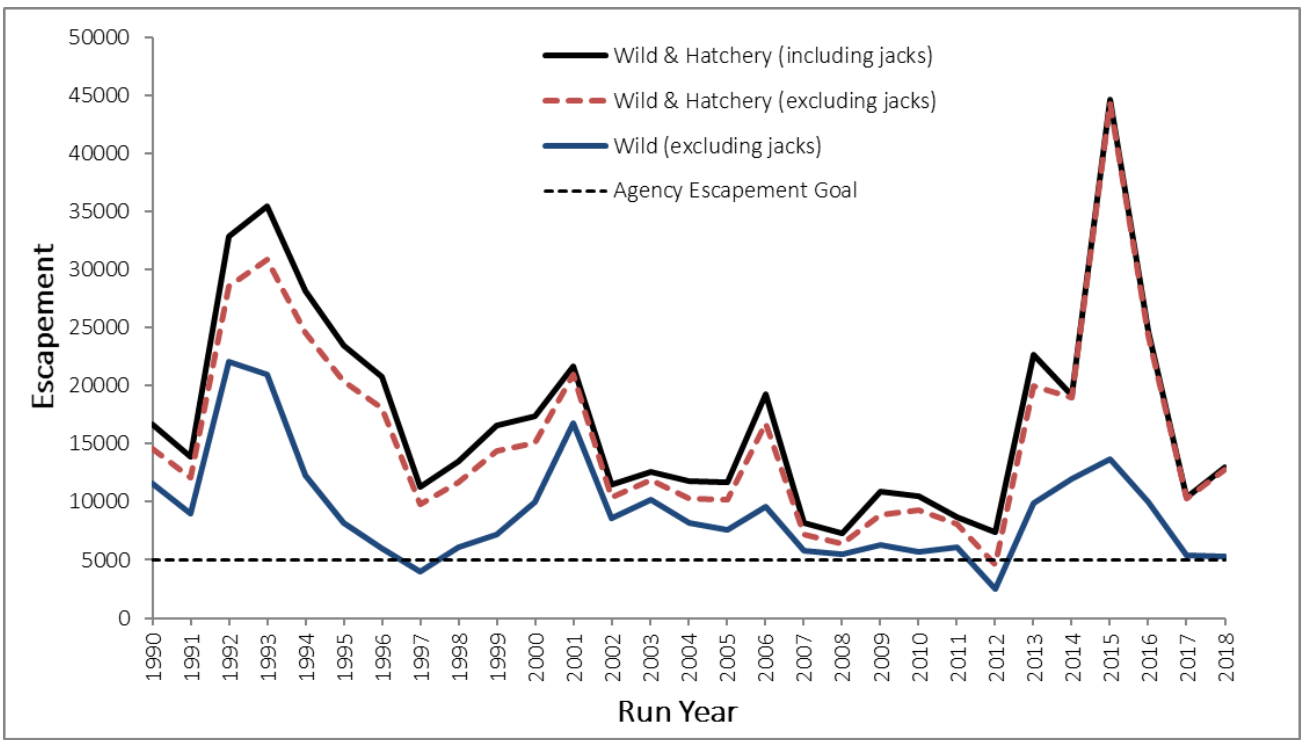

Figure 4. 1990 to 2018 Atnarko Chinook escapement

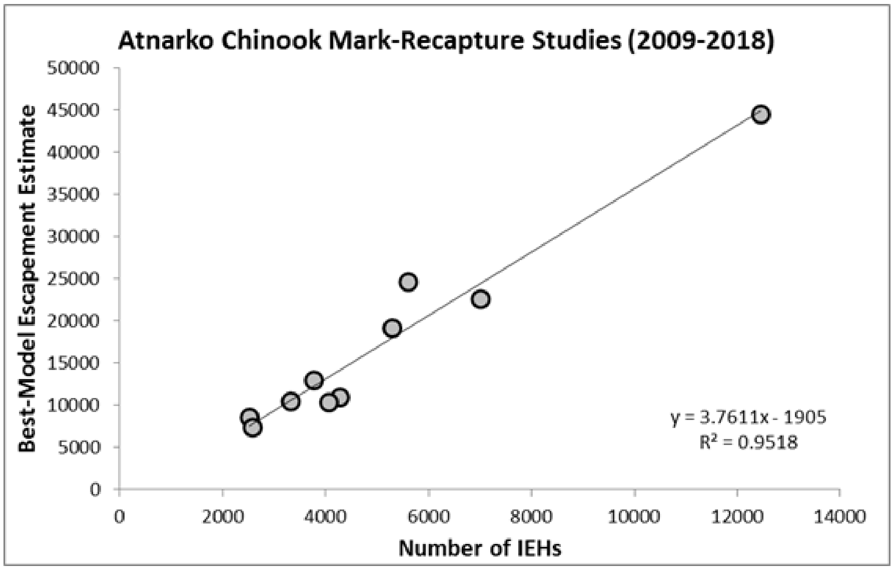

Figure 5. Relationship between IEH and escapement estimate

TABLES

Table 1. Atnarko Chinook MLE Escapement.
*2004 to 2008 estimates are based on time series calibration (Vélez-Espino *et al*. 2014).

Year	Estimate	CV	Large Wild Atnarko Chinook Salmon
2001	**21,635**	**0.034**	**16,743**
2002	**11,511**	**0.084**	**8,550**
2003	**12,619**	**0.055**	**10,136**
2004	*11,825*	*0.089*	*8,230*
2005	*11,677*	*0.110*	*7,619*
2006	*19,288*	*0.156*	*9,565*
2007	*8,229*	*0.061*	*5,799*
2008	*7,288*	*0.073*	*5,517*
2009	**10,926**	**0.047**	**6,331**
2010	**10,497**	**0.059**	**5,683**
2011	**8,645**	**0.071**	**6,061**
2012	**7,425**	**0.060**	**2,542**
2013	**22,690**	**0.047**	**9,860**
2014	**19,180**	**0.046**	**11,935**
2015	**44,594**	**0.120**	**13,640**
2016	**24,234**	**0.047**	**9,936**
2017	**10,308**	**0.046**	**5,418**
2018	**13,008**	**0.078**	**5328**

Table 2: Summary of encounter histories for the 2018 Atnarko Mark-Recapture Experiment.

Year	Sex	Tags Applied	Tags Recovered	Carcasses Examined	Number of Encounter Histories *a*
	F	207	19	623	1407
2018	M	1086	93	770	2331
	J	16	0	2	18
	Total	**1309**	**112**	**1395**	**3756**

Table 3. Results from closure tests. Notation is explained in Vélez-Espino et al. (2010).

```
                          Stanley & Burnham Closure Test
                 (Low p-values suggest population not closed):

Chi-square statistic= 400.56637
df= 18.
p-value= 0.00000

                          Otis et al. (1978) Closure Test
                 (Low p-values suggest population not closed):

z-value=    -3.07729
p-value=     0.00104


 Component Statistics of Stanley & Burnham Closure Test
-------------------------------------------------------------------------------
     Component   Chi-square             df           p-value
-------------------------------------------------------------------------------
 Tests for additions to population (Low p-values suggest there were additions)
      NR vs JS   239.04210               9.          0.00000
     M_t vs NM   344.50395              10.          0.00000

 Tests for losses from population (Low p-values suggest there were losses)
     M_t vs NR   161.52427               9.          0.00000
      NM vs JS    56.06243               8.          0.00000
-------------------------------------------------------------------------------
```

Table 4. Open population model selection using AIC

Models are defined by the probability of capture (p), the probability of survival (s), and the probability of entering the system (b) under time-specific (t), group-specific (g), time and group-specific (g*t), and/or invariant (*) conditions. Best model is the one with the lowest AIC.

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	#Par	Deviance
{p(g), s(g,t), b(g,t)}	4486.5	0.0	0.99998	1	66	-13550.8
{p(g,t), s(g,t), b(g,t)}	4508.6	22.0	0.00002	0	90	-13581.4
{p(*), s(g,t), b(g,t)}	4515.6	29.0	0	0	64	-13517.5
{p(g), s(g,t), b(t)}	4521.8	35.2	0	0	46	-13472.9
{p(*), s(g), b(g,t)}	4579.3	92.8	0	0	37	-13396.4
{p(g), s(g), b(g,t)}	4597.4	110.8	0	0	39	-13382.5
{p(*), s(*), b(g,t)}	4599.1	112.6	0	0	35	-13372.4
{p(g), s(*), b(g,t)}	4625.1	138.5	0	0	37	-13350.6
{p(*), s(*), b(t)}	4665.2	178.7	0	0	15	-13265.1