

Fishery Data Series No. 19-10

Bering Cisco Spawning Abundance in the Upper Yukon Flats, 2016–2017

by

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Alaska Department of Fish and Game

Divisions of Sport Fish and Commercial Fisheries



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Weights and measures (metric)		General		Mathematics, statistics	
centimeter	cm	Alaska Administrative Code		all standard mathematical signs, symbols and abbreviations	
deciliter	dL		AAC		
gram	g	all commonly accepted abbreviations	e.g., Mr., Mrs., AM, PM, etc.	alternate hypothesis	H _A
hectare	ha			base of natural logarithm	e
kilogram	kg			catch per unit effort	CPUE
kilometer	km	all commonly accepted professional titles	e.g., Dr., Ph.D., R.N., etc.	coefficient of variation	CV
liter	L			common test statistics	(F, t, χ^2 , etc.)
meter	m	at	@	confidence interval	CI
milliliter	mL	compass directions:		correlation coefficient (multiple)	R
millimeter	mm	east	E	correlation coefficient (simple)	r
Weights and measures (English)		north	N	covariance	cov
cubic feet per second	ft ³ /s	south	S	degree (angular)	°
foot	ft	west	W	degrees of freedom	df
gallon	gal	copyright	©	expected value	E
inch	in	corporate suffixes:		greater than	>
mile	mi	Company	Co.	greater than or equal to	≥
nautical mile	nmi	Corporation	Corp.	harvest per unit effort	HPUE
ounce	oz	Incorporated	Inc.	less than	<
pound	lb	Limited	Ltd.	less than or equal to	≤
quart	qt	District of Columbia	D.C.	logarithm (natural)	ln
yard	yd	et alii (and others)	et al.	logarithm (base 10)	log
Time and temperature		et cetera (and so forth)	etc.	logarithm (specify base)	log ₂ , etc.
day	d	exempli gratia		minute (angular)	'
degrees Celsius	°C	(for example)	e.g.	not significant	NS
degrees Fahrenheit	°F	Federal Information Code	FIC	null hypothesis	H ₀
degrees kelvin	K	id est (that is)	i.e.	percent	%
hour	h	latitude or longitude	lat or long	probability	P
minute	min	monetary symbols		probability of a type I error	
second	s	(U.S.)	\$, ¢	(rejection of the null hypothesis when true)	α
Physics and chemistry		months (tables and figures): first three letters	Jan,...,Dec	probability of a type II error	
all atomic symbols		registered trademark	®	(acceptance of the null hypothesis when false)	β
alternating current	AC	trademark	™	second (angular)	"
ampere	A	United States		standard deviation	SD
calorie	cal	(adjective)	U.S.	standard error	SE
direct current	DC	United States of America (noun)	USA	variance	
hertz	Hz			population	Var
horsepower	hp	U.S.C.	United States Code	sample	var
hydrogen ion activity (negative log of)	pH				
parts per million	ppm	U.S. state	use two-letter abbreviations		
parts per thousand	ppt, ‰		(e.g., AK, WA)		
volts	V				
watts	W				

FISHERY DATA SERIES NO. 19-10

**BERING CISCO SPAWNING ABUNDANCE IN THE UPPER YUKON
FLATS, 2016-2017**

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ABSTRACT

This project estimated the abundance of spawning Bering cisco (*Coregonus laurettae*) in a 125 km reach of the Yukon River between Circle and the mouth of the Porcupine River in fall 2016 and 2017. Fish were captured utilizing boat-based electrofishing and abundance was estimated using a two-event Petersen mark-recapture model (with Bailey's modification) for a closed population. Evaluation of experimental assumptions and diagnostics tests indicated that no stratification by size, sex, or area was needed in 2016, whereas stratification by sex and size was required in 2017. Bering cisco spawning abundance was estimated as 387,326 (SE = 37,200) in 2016 and 387,042 (SE = 42,181) in 2017. In both study years, movements of recaptured fish and previous telemetry studies suggest that there was immigration into the study area between events, making these abundance estimates germane to the second event. Females were predominantly age-5–7, whereas males were predominantly age-4–5. Gonadosomatic indices collected from female fish indicated that all were in spawning condition.

Key words: Bering cisco, *Coregonus laurettae*, Yukon River, Yukon Flats, Porcupine River, Fort Yukon, Circle, mark-recapture, abundance, length composition

INTRODUCTION

Bering cisco (*Coregonus laurettae*) are widely distributed in coastal habitats of western Alaska but only spawn in the Yukon and Kuskokwim rivers (McPhail 1966; Alt 1973; Brown et al. 2012a). A spawning population has also been documented in the Susitna River in southcentral Alaska (ADF&G 1983), but it is unlikely that individuals from that population would range into the Bering Sea. Residents of coastal communities in western Alaska highly value Bering cisco because of its high oil content and flavor (Stickney 1984; Runfola 2011). Although quantitative data describing subsistence harvests of Bering cisco is limited, harvests make up a substantial component of annual whitefish *Coregonus sp.* and sheefish *Stenodus leucichthys* harvests from the Yukon River. From 2008 through 2017, subsistence surveys from 9 communities (1–6 communities surveyed each year) in the Lower Yukon River and Yukon River Delta areas showed that ciscoes (Bering and least cisco were not differentiated) composed on average 17% of all whitefish and sheefish harvested (Fall et al. 2012; Ikuta et al. 2014; Brown et al. 2015; Ikuta et al. 2016; Runfola et al. 2018; Godduhn et al. 2020).

Beginning in 2005, a commercial fishery for Bering cisco developed at the mouth of the Yukon River that supplies a market in New York City (Fabricant 2008; Demarban 2010; Brown et al. 2012a). Initially the commercial fishery harvest quota was set at 10,000 lb (~9,250 fish) in 2005 and has incrementally increased to a current quota of 35,000 fish (~40,000 lb) in 2018, and it will remain at that level through 2020 (D. Jallen, Fishery Biologist, ADF&G, Anchorage, memorandum, March 2019). On average, the fishery harvests about 90% of the yearly allowable quota. In the past, the deep-water cisco fisheries in the Laurentian Great Lakes supplied the New York City market, but those species have been depleted by overfishing, impacted by environmental changes, and displaced by invasive species making them no longer viable (Hoff and Todd 2004; Gorman and Todd 2007; Bronte et al. 2010). The market in New York City is large and there is considerable pressure on the Alaska Department of Fish and Game (ADF&G) to expand the commercial harvest allocation for Bering cisco to provide increased economic opportunity for residents of the Yukon Delta and a larger supply of product to the market.

In response to the Yukon Delta commercial fishery, several research projects have been undertaken to examine the basic life history and migratory patterns of Bering cisco. The spawning population in the Yukon River is composed primarily of individuals between the ages of 5 and 7 years, with very few fish younger than 4 or older than 8 years (Brown et al. 2012a). In contrast, the commercial fishery harvests non-spawning fish that are predominantly immature (mode = 4 years).

All historical sampling data within the Yukon River drainage and telemetry data indicate that Yukon River Bering cisco spawn in a single region of the Yukon River centered in the Upper Yukon Flats (Figure 1; Brown et al. 2012a; Brown and Daum 2015; R. J. Brown, USFWS, unpublished data). Based on data collected at an experimental fish wheel located on the Yukon River at Rapids (rkm 1,176; Rapids Research Center, Box 172, Tanana, Alaska 99777, USA), the upstream migration of pre-spawning Bering cisco begins before mid-June, when the fish wheel typically becomes operational; continues with multiple pulses through August; and declines by early September (Brown et al. 2012b). While the first fish in the annual spawning migration pass Rapids earlier than mid-June, it is not clear whether the early migrants represent a large or small fraction of the run. Migration speeds along the river have been estimated for a small number of radiotagged Bering cisco, averaging 13 km·d⁻¹ (Brown and Daum 2015). If this migration speed is common through the early and late parts of the run, Bering cisco must begin migrating upstream under ice by mid-March to pass Rapids by mid-June.

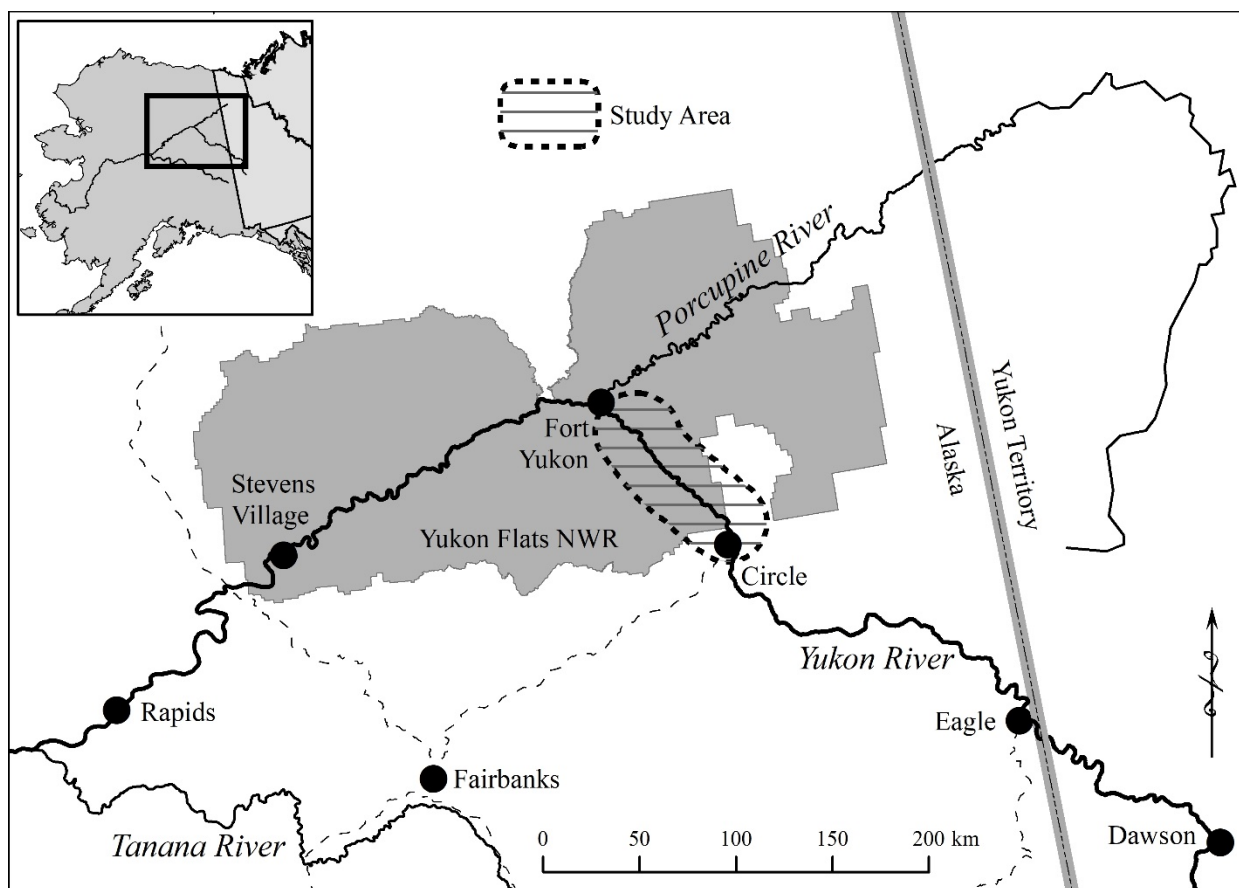


Figure 1.—Map depicting the Yukon Flats, Rapids, and mark-recapture study area.

The most recent telemetry project was conducted to delineate the geographic spawning distribution of the Bering Cisco population in the Yukon River upstream of Rapids (Brown and Daum 2015). Seventy-nine percent spawned in the Upper Yukon Flats (between Fort Yukon and Circle), upstream from the mouth of the Porcupine River, and 21% spawned in the Lower Yukon Flats (between Stevens Village and Fort Yukon). From the telemetry data it was inferred that most spawning took place during the second and third weeks of October. Possible spawning areas downstream of Rapids were not investigated, but it is thought that spawning in these locations is

unlikely due to a lack of suitable habitat (i.e., shallow and braided river channels that are unique to the Yukon Flats portion of the Yukon River; Brown and Daum 2015).

Although prior research has delineated the temporal and geographic extent of the Bering cisco spawning population, management agencies still have no estimate of population size. Given the growing extent of the commercial fishery, ADF&G undertook a 2-year examination of the Yukon River Bering cisco spawning population in the Upper Yukon Flats to determine abundance and describe age, sex, and length compositions. This was the first attempt to produce an abundance estimate for this population, or any population, of Bering cisco. This report describes a two-event mark-recapture project using boat electrofishing as a capture mechanism between mid-September and mid-October that estimated the abundance of Bering Cisco in the Upper Yukon Flats in 2016 and 2017.

OBJECTIVES

The research objectives for this study were to:

1. Estimate the abundance of spawning Bering cisco in a 125 km reach of the Upper Yukon Flats in early October of 2016 and 2017, such that estimates were within 25% of the true abundance 90% of the time;
2. Estimate length and sex compositions of spawning Bering cisco in a 125 km reach of the Upper Yukon Flats such that all proportion estimates were within 5 percentage points of the true proportion values 95% of the time; and
3. Estimate the age composition of spawning male and female Bering cisco (separately) in a 125 km reach of the Upper Yukon Flats such that all proportion estimates were within 10 percentage points of the true proportion values 95% of the time.

A secondary research objective for this study was to:

1. Measure gonadosomatic indices (GSI) from all female fish from which age structures were collected to assess sexual maturity and spawning readiness.

METHODS

STUDY AREA

The study area encompasses the entire Upper Yukon Flats. It is approximately 125 km in length, extending from a point 10 km upstream of Circle to the mouth of the Porcupine River at Fort Yukon. In this reach, the Yukon River arcs through the flats, flowing from east to west. The current is swift with generally turbid water through a heavily braided floodplain composed of gravel, sand, and silt (Figure 1).

To facilitate distribution of sampling effort, the study area was divided into 10 sections, each approximately 12.5 km in length. The length of each section corresponded to the amount of river that could realistically be sampled within one day and provided a meaningful geographic scale for diagnostic testing.

OVERVIEW

This study was designed to estimate abundance in the 125 km sampling area using two-event Petersen mark-recapture (M-R) techniques for a closed population (Seber 1982) designed to satisfy the following assumptions:

1. the population is closed (Bering cisco do not enter the population, via growth or immigration, or leave the population, via death or emigration, during the experiment);
2. all Bering cisco will have a similar probability of capture in the first event or in the second event, or marked and unmarked fish will mix completely between events;
3. marking of Bering cisco will not affect the probability of capture in the second event;
4. marked Bering cisco will be identifiable during the second event; and
5. all marked Bering cisco will be reported when recovered in the second event.

Failure to satisfy these assumptions may result in biased estimates, therefore the experiment was designed to satisfy or provide the capacity to test these assumptions. Sufficient data were collected to perform diagnostic tests to identify heterogeneous capture probabilities (violations of assumption 2) and prescribed model selection procedures were followed in the event of such violations (Appendix A1). Diagnostic tests are not available to evaluate assumptions 1, 3, 4, and 5.

We anticipated that the population of inference would not be closed (assumption 1). Based upon previous telemetry research, it is likely that one-way immigration occurred through the downstream study area boundary between sampling events. This violation indicates that the estimates of abundance are germane to the population within the study area during the second event provided no emigration occurred concurrently. It was expected that abundance estimates from the second event would encapsulate the entire spawning population within the study area barring significant emigration through the upper boundary of the study area. To examine how possible emigration from the population through the upstream study area boundary would affect abundance estimates, we calculated a Petersen mark–recapture estimate for open rivers (Evenson 1987; Appendix C) and compared it to the population abundance estimate identified by diagnostic tests.

To ensure equal probabilities of capture and adequate mixing (assumption 2), we relied on a combination of systematic sampling and a hiatus of sufficient length between sampling events. The first event occurred during early- to mid-September when most (i.e., >80%) Bering cisco had entered the study area but were still moving upstream to spawning locations. The second event occurred between late September and early October when fish were at their spawning areas and just beginning to spawn. The hiatus between the sampling events was 15 days, which allowed for partial mixing and—along with the systematic sampling protocols—ensured that assumption 2 was satisfied. This general approach was successfully applied on the Chatanika River to estimate abundance of humpback whitefish (Wuttig 2009).

We could not test assumptions 3, 4, and 5, but the experiment was designed to give a reasonably high probability that they were not violated. Captured fish were shocked at optimal amperage and were tagged and released quickly, which minimized handling and tag-induced effects on behavior (assumption 3). Furthermore, the hiatus was assumed to be of sufficient length to allow marked fish to recover from the effects of capture and handling. Use of secondary marks and diligent inspection of fish sampled in the second event ensured all marked fish were identified and reported (assumptions 4 and 5).

SAMPLING

The first sampling events occurred from 10–19 September 2016 and 10–20 September 2017, and the second events occurred from 24 September–4 October 2016 and 25 September–5 October 2017. The second events occurred prior to any emigration of radiotagged Bering cisco observed in 2012–2013 (approximate range between October 15 and November 1; Brown and Daum 2015).

For all sampling events, 2 boats equipped with electrofishing gear were used to capture Bering cisco. Each boat had a 3-person crew with one person piloting the boat and operating the electrofishing gear and 2 using dip nets to capture fish that were shocked by the gear. Each boat was equipped with a pulsed-DC variable-voltage pulsator (Coffelt Model VVP-15) powered by a 5,000-watt single-phase gasoline generator. Anodes consisted of four 15 mm diameter steel cables (1.5 m long) spaced 1 m apart and arranged perpendicular to the long axis of the boat and 2.1 m forward of the bow. The unpainted bottom of the boat served as the cathode. The electrical output (voltage, amperage, and cycle) was adjusted based on observed responses of shocked fish. To minimize fish mortality and injury, electrical output values were adjusted to minimize exposure to zones of tetany (Snyder 1992). Initially, settings on the pulsator were set at 50% duty cycle and 30 Hz. Because output amperage varies at a given voltage due to conductivity, substrate, and water depth, the boat operator adjusted voltage (250–300 V) to keep output between 2 and 4 amperes.

The Yukon River is immense and an electrofishing boat can only sample a very small portion of a study section. However, sampling took advantage of the telemetry data (Brown and Daum 2015) and the known behavior of Bering cisco to focus sampling effort on areas of higher fish densities in each sampling section. To improve sampling efficiency, detailed section maps of Bering cisco spawning locations from 2012 and 2013 were utilized to identify that reaches and river channels had the highest concentrations of fish. Each electrofishing boat was assigned half of the river or channel. When 2 channels existed, each boat was assigned a channel. If 3 or more existed, the 2 largest were sampled, and if the telemetry maps indicated that the additional channel(s) had significant spawning aggregations or habitat, the boat(s) also sampled those channels.

Attempts were made to systematically and uniformly distribute effort over each study section by operating the electrofishing boats in 5- to 20-minute intervals (runs) and focusing on the stream margins. The duration of each run was adjusted based on catch rates (i.e., once the sampling tub is full; approximately 40–60 fish), but did not exceed 20 min. During each event, the beginning and end points of all runs were recorded using a hand-held GPS unit. Runs also ended at sectional boundaries regardless of run duration.

Captured fish were sampled immediately after completing a run. During the first event all Bering cisco were double marked using individually numbered Floy¹ tags (primary mark) and a partial clip of the upper caudal fin (secondary mark). To prevent resampling during the second event, all sampled fish received a lower caudal fin clip.

All fish captured in both events were measured for length (mm FL) and sexed. During spawning, sex can be determined from secondary characteristics and expulsion of sex products. Sample sizes for the mark-recapture experiment were determined using the methods of Robson and Regier (1964) and sample sizes for Objectives 2 (length and sex composition) and 3 (age composition) were determined using the methods of Thompson (1987) and Cochran (1977).

During each of the second event sampling days, 15 fish of each gender were randomly collected and sampled for age and maturity. Otoliths were collected for aging, providing a total of 150 otoliths from each sex, which exceeded the required sample size to address Objective 3. Otoliths were placed into labeled coin envelopes that were cross-referenced with the data forms. Ages were determined as described by Brown (2000). Otoliths were collected in lieu of scales because ages from scales are not as accurate as those from otoliths (Andy Padilla, Fisheries Biologist, ADF&G,

¹ Product names are included for scientific completeness and do not constitute product endorsement.

Fairbanks, memorandum, June 2015). Additionally, fish from which otoliths were collected were weighed and gonad weights were collected from females to calculate GSI and assess maturity. Female coregonids with GSI values >3% indicate fish are sexually mature and will spawn that year (Moulton et al. 1997; Brown 2004, Brown et. al 2007). All weights were measured to the nearest 10 g.

DATA ANALYSIS

Objective 1 – Abundance

Differences in capture probability related to fish size, sex, and location were examined (assumption 2). Size-selective sampling was tested using Kolmogorov-Smirnov tests, and sex-selective sampling was investigated using chi-square tests. These tests and possible stratification decisions are outlined in Appendix A1. If stratification by size or sex was required, the abundance estimates and associated variances would be summed across strata.

Spatial violations of assumption 2 were tested using consistency tests described by Seber (1982; Appendix A2). Assumption 2 would be satisfied if at least 1 of the 3 consistency tests outlined in Appendix A2 failed to reject the associated null hypothesis. If all 3 of these tests rejected the null hypothesis a partially or completely stratified estimator would be used. If no movement of marked Bering cisco between geographic strata was observed, a completely stratified abundance estimate would be computed using the methods of Bailey (1951, 1952). If there was some movement of marked Bering cisco between strata but mixing was incomplete, the methods of Darroch (1961) would be used to compute a partially stratified abundance estimate.

When diagnostics indicated incomplete mixing, a stratified abundance estimator (Darroch 1961) was used. The R package SPAS-2 was used to estimate maximum-likelihood abundance and associated variance (Carl Schwarz, Statistics and Actuarial Science, Simon Fraser University, personal communication). To reduce the frequency of 0-count cells in the tag-recovery matrix (Appendix B), adjacent spatial strata were pooled. A series of 8 models were estimated in which the probability of capture in the tagging and recovery strata were constrained in different ways with the probabilities of capture always constrained in a contiguous manner. For example, in 1 of the 8 models the probability of capture might be constrained as equal for marking strata 1 through 3, but not for strata 4 and 5. All 8 models were compared with Akaike's Information Criterion (AIC; Burnham and Anderson 2002) and the best supported model was selected for generating the abundance estimate.

If none of the assumptions were violated, the abundance of Bering cisco in the 125 km study area would be estimated using Bailey's modification of the Petersen estimator (Bailey 1951, 1952). This estimator was used because the sampling design calls for a systematic downstream progression and in effect results in sampling with replacement.

The Bailey estimator and its estimated variance were:

$$\hat{N} = \frac{n_1(n_2 + 1)}{(m_2 + 1)} \quad (1)$$

$$\text{var}(\hat{N}) = \frac{n_1^2(n_2 + 1)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)} \quad (2)$$

where:

n_1 = the number marked during the first sampling event;

n_2 = the number examined during the second sampling event; and

m_2 = the number captured during the second sampling event with marks

Objectives 2 and 3 – Length, sex, and age composition

For cases I–III (Appendix A1), where stratification is not necessary, age, sex, and length proportions (10 mm length categories) and their variances were estimated using samples from the event(s) without size-selectivity as follows:

$$\hat{p}_k = \frac{n_k}{n} \quad (3)$$

where:

\hat{p}_k = proportion of fish that were within age, sex, or length category k ;

n_k = the number of fish sampled that were within age, sex, or length category k ; and

n = the total number of fish sampled for age, sex, or length.

The unbiased variance of this proportion was estimated as (Cochran 1977):

$$\text{var}[\hat{p}_k] = \frac{\hat{p}_k(1 - \hat{p}_k)}{n - 1} \quad (4)$$

If the diagnostic tests outlined in Appendix A1 indicated case IV (size-selectivity during both events), data were stratified to eliminate variability in capture probabilities within strata for at least one or both sampling events. Formulae to adjust length or sex composition estimates are presented in Appendix A1 (Equations 1–3).

Secondary Objective 1 – Gonadosomatic indices

GSI of female fish were calculated as follows:

$$GSI_i = \frac{G_i}{S_i} * 100 \quad (5)$$

where:

GSI_i = gonadosomatic index of female fish i ;

G_i = gonad weight of female fish i ; and,

S_i = whole-body weight of female fish i .

RESULTS

2016 STUDY

Summary

A total of 5,037 Bering cisco were marked in the first event (n_1), and 8,150 fish were examined (n_2) during the second event, of which 105 were recaptures (m_2 : Appendix B1). Of all recaptured Bering cisco, one had lost its tag and was identified by its fin clip. Otoliths were collected from

316 individuals and GSI were collected from 155 female Bering cisco during the second sampling event.

Evaluation of Assumptions

We believe there was immigration into the population (violation of assumption 1) from the river section downstream of the study area as fish migrated to spawning grounds. The tag-recovery matrix (Appendix B1) demonstrated consistent movement of tagged fish upstream from marking strata, with very little downstream movement (zero values are substantially more prevalent in the upper right off-diagonal elements compared to lower left off-diagonal elements). Provided there was no emigration, immigration in a two-event mark-recapture experiment indicates that the abundance estimate was germane to the second event. Additionally, the Petersen abundance estimate for open rivers (Evenson 1987), modified for emigration through the upper boundary only, was within 3% of the Petersen-style estimate (Appendix C). This argument is augmented by telemetry data (Brown and Daum 2015) that suggests immigration into the population from downstream and minimal movement of tagged fish beyond the upstream boundary of the study area.

Diagnostic tests (Appendix A1 and A2) indicated that no size stratification was required and a Petersen-type model was appropriate for the 2016 abundance estimation. Size-based variability in capture probability was not detected in the first event (KS D-statistic = 0.071; $p = 0.54$), although it was detected in the second event (KS D-statistic = 0.13; $p = 0.04$) and fish lengths varied significantly between sampling events (KS D-statistic = 0.11; $p < 0.01$). Capture probabilities did not vary by sex in either event (event 1: $\chi^2 = 0.03$, $df = 1$; $p = 0.85$; event 2: $\chi^2 = 2.62$, $df = 1$; $p = 0.11$), indicating that sex-stratification was not required. The ratios of marked to unmarked fish varied significantly among sampling sections ($\chi^2 = 14.01$, $df = 4$; $p < 0.01$) and fish failed to mix completely at $\alpha = 0.08$ ($\chi^2 = 8.4$, $df = 4$; $p = 0.08$). To be conservative, we implemented a Darroch-type model, but we found the estimate was within 5% of the Petersen-type estimate and thus present the Petersen estimate as final.

Abundance Estimate

Using the Bailey's modification of the Petersen estimator, an abundance of 387,326 (SE = 37,200) Bering cisco was estimated within the study area. Upper and lower 95% confidence intervals were 460,238 and 314,414 fish, respectively. Relative precision was 0.19 at $\alpha = 0.05$.

Length, Sex, and Age Composition

Sex and length composition were calculated using data from both events (Figure 2 and Table 1). Sex composition was estimated as 74.5% male (SE = 0.4%) and 25.5% female (SE = 0.04%). Sex selectivity was not detected in the first or second sampling events ($\chi^2 = 0.03$, $df = 1$, $p = 0.85$ and $\chi^2 = 2.6$, $df = 1$, $p = 0.11$, respectively). Length selectivity in the first or second events was not detected in males (KS D-statistic = 0.09; $p = 0.46$, KS D-statistic = 0.1; $p = 0.35$, respectively) or females (KS D-statistic = 0.22; $p = 0.11$, KS D-statistic = 0.22; $p = 0.13$, respectively).

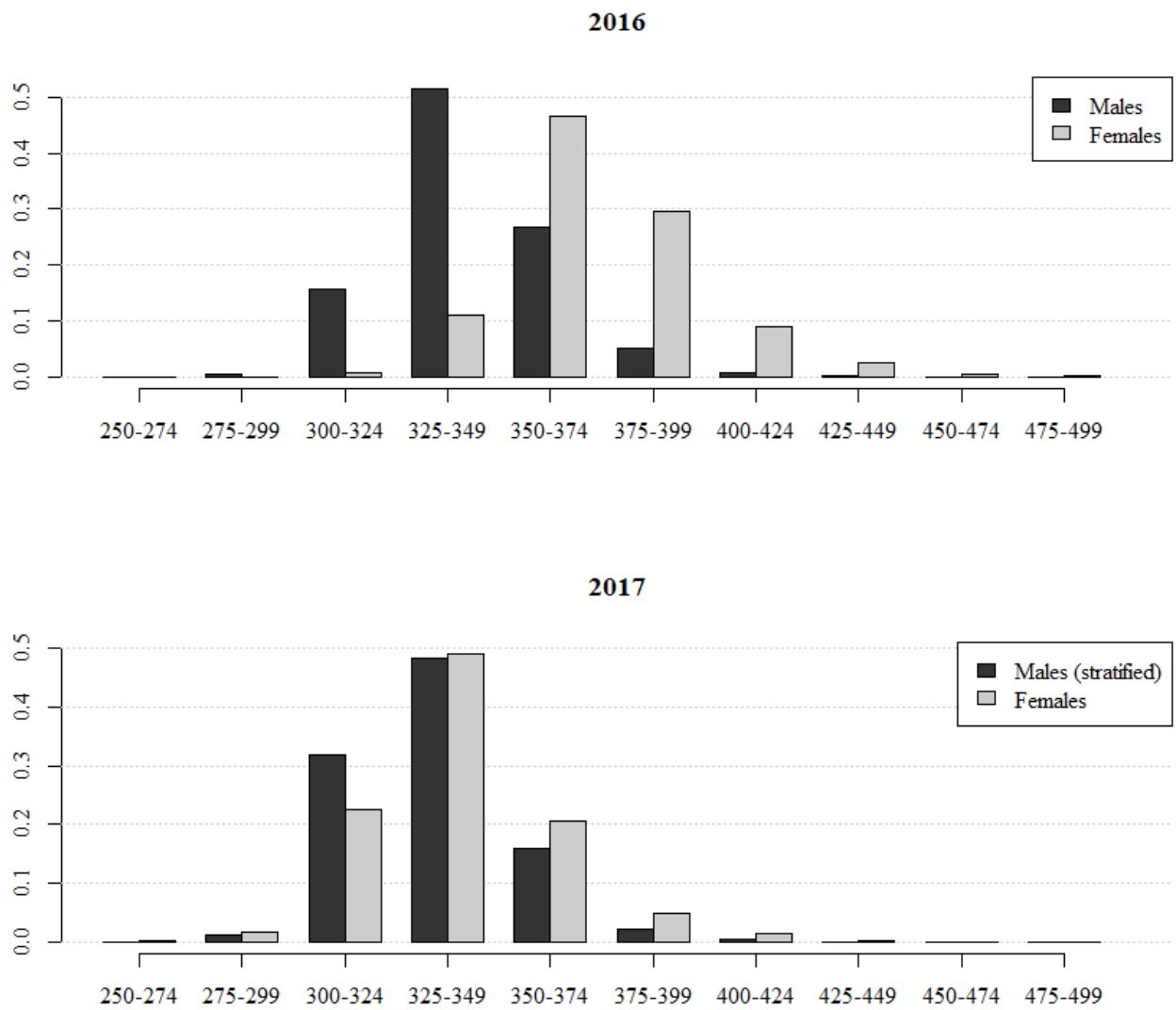


Figure 2.—Length distribution of male and female Bering cisco in the Upper Yukon Flats in 2016 and 2017.

Table 1.—Length-at-age and age distribution of Bering cisco in the Upper Yukon flats in 2016.

Sex	Age	<i>n</i>	Size Range (FL mm)	Mean (FL mm)	Proportion Age x	SE(P(Age))
Females	3	1	N/A	400	0.01	0.008
	4	19	339-415	364	0.13	0.027
	5	26	342-438	370	0.17	0.031
	6	52	350-440	383	0.34	0.039
	7	37	354-423	383	0.25	0.035
	8	8	360-462	401	0.05	0.018
	9	5	378-440	406	0.03	0.014
	10	1	N/A	412	0.01	0.008
	11	2	400-413	407	0.01	0.008
Males	3	8	307-358	333	0.05	0.017
	4	58	300-367	335	0.36	0.038
	5	36	305-414	345	0.23	0.033
	6	25	321-380	351	0.16	0.029
	7	17	324-393	357	0.11	0.025
	8	6	333-390	358	0.04	0.016
	9	5	322-400	361	0.03	0.014
	10	3	350-365	355	0.02	0.011
	11	1	N/A	341	0.01	0.008

Gonadosomatic Indices

GSI were calculated from 155 female Bering cisco and ranged between 16–43% (mean = 29%, SE = 0.4%).

2017 STUDY

Summary

A total of 4,516 Bering cisco were marked in the first event (n_1), and 10,154 fish were examined (n_2) during the second event, of which 131 were recaptures (m_2 ; Appendix B2). Otoliths were collected from 316 individuals and GSI were collected from 155 female Bering cisco during the second sampling event.

Evaluation of Assumptions

As in 2016, we believe there was immigration into the population (violation of assumption 1) from the river section downstream of the study area as fish migrated to spawning grounds. The tag-recovery matrix (Appendix B2) demonstrated consistent movement of tagged fish upstream from tagging strata, with very little downstream movement. Provided there is no emigration, immigration in a two-event mark–recapture experiment indicates that the abundance estimate is germane to the second event. The Petersen abundance estimate for open rivers (Evenson 1987; Appendix C), modified for emigration through the upper boundary only, was within 6% of the sex-stratified Bailey estimate.

Diagnostic tests (Appendices A1 and A2) indicated that a sex-stratified Bailey estimator was most appropriate and that the estimates for males should be stratified by length. For large males, a Darroch-type model was found to be most appropriate. Capture probabilities varied significantly

by sex in both events ($\chi^2 = 4.0$, $df = 1$; $p = 0.04$ and $\chi^2 = 9.91$, $df = 1$; $p < 0.01$). After stratification by sex, capture probabilities of males varied significantly by size in both events (KS D-statistic = 0.13; $p = 0.03$ and KS D-statistic = 0.13; $p = 0.02$), whereas there was no evidence that lengths of males varied significantly between events (KS D-statistic = 0.01; $p = 0.86$). The stratification point for males suggested by the KS tests was 325 mm. For females, there was no evidence of size selectivity in the first (KS D-statistic = 0.19; $p = 0.34$) or second event (KS D-statistic = 0.21; $p = 0.28$). Lengths of females also did not vary between events (KS D-statistic = 0.04; $p = 0.07$). Additionally, there was evidence of complete mixing in both the female and small male (≤ 325 mm FL) populations ($\chi^2 = 3.6$, $df = 4$; $p = 0.47$ and $\chi^2 = 4.30$, $df = 4$; $p = 0.37$) and that the ratio of marked to unmarked individuals did not vary significantly among sampling sections for those populations ($\chi^2 = 3.4$, $df = 4$; $p = 0.51$ and $\chi^2 = 3.5$, $df = 4$; $p = 0.48$). However, the marked to unmarked ratio of large males (> 325 mm FL) varied significantly among sampling sections in the second event ($\chi^2 = 19.9$, $df = 4$; $p < 0.01$) and failed to mix completely ($\chi^2 = 12.5$, $df = 4$; $p = 0.01$) thus indicating that a Darroch-type estimator was most appropriate.

Abundance Estimate

Based on the stratification decisions described above, the abundance estimate for 2017 consisted of Bailey estimates for females and small (< 325 mm) males and a Darroch-type estimate for large (> 325 mm) males. The estimate of total abundance of Bering cisco in the Upper Yukon Flats in 2017 was 387,042 (SE = 42,181). Relative precision was 0.21 at $\alpha = 0.05$, and the symmetric 95% confidence interval was 304,368 to 469,716. Abundance of females was estimated at 139,425 (SE 29,366) and the abundance of small males (< 325 mm) was estimated at 91,896 (SE 18,662). For large males the Darroch estimate was 155,721 (SE = 23,845). The best supported model was one with equal probability of capture for marking and recapture strata 1–2, with changing probability of capture for strata 3, 4, and 5.

Length, Sex, and Age Composition

Sex and length compositions were calculated using data from both events (Figure 2 and Table 2). The sex composition was estimated as 64% male (SE = 5.6%) and 36% female (SE = 5.6%). Sex selectivity was detected for the first and second events in 2017 ($\chi^2 = 4.0$, $df = 1$, $p = 0.04$ and $\chi^2 = 9.9$, $df = 1$, $p < 0.01$). Length selectivity was detected in males for both events in 2017 (KS D-statistic = 0.13, $p = 0.03$; and KS D-statistic = 0.13, $p = 0.03$, respectively) but not in females in either event (KS D-statistic = 0.19, $p = 0.34$; and KS D-statistic = 0.21, $p = 0.28$, respectively).

Gonadosomatic Indices

GSI were calculated from 157 female Bering cisco. GSI values ranged between 16% and 58% (mean = 27%, SE = 0.35%).

Table 2.—Summary of age and length data for Bering cisco collected during the second sampling event in 2017.

Sex	Age	<i>n</i>	Size Range (FL mm)	Mean (FL mm)	Proportion Age x	SE(P(Age))
Females	4	21	322-385	356	0.13	0.027
	5	60	332-458	368	0.38	0.039
	6	29	339-446	381	0.19	0.032
	7	19	362-426	384	0.12	0.026
	8	20	357-480	390	0.13	0.027
	9	3	373-443	400	0.02	0.011
	10	1	N/A	397	0.01	0.008
	11	1	N/A	415	0.01	0.008
	12	2	420-448	434	0.01	0.008
Males	3	3	299-335	315	0.03	0.019
	4	47	300-386	337	0.36	0.045
	5	56	304-374	340	0.39	0.045
	6	20	318-378	347	0.14	0.031
	7	6	334-376	355	0.03	0.013
	8	8	327-398	365	0.04	0.015
	12	1	N/A	388	0.01	0.006

DISCUSSION

This study provides the first abundance estimate of Bering cisco in the Yukon River drainage. This project demonstrated that under certain conditions, boat-based electrofishing can be an effective way to sample large numbers of fish in large, braided river habitats. The success of this work was greatly aided by data from Brown and Daum's (2015) telemetry study. Location data from their study were used to delineate study area boundaries, assess periods of potential population closure, and direct sampling effort within the study area. The telemetry data also indicate that our abundance estimates should be considered minimum estimates of abundance in the Yukon Flats. Telemetry data indicated 79% of Bering cisco spawn in the reach of river sampled here while the remaining 21% primarily spawn downstream of the study area (Brown and Daum 2015).

Immigration likely occurred across the downstream study area boundary in both study years, but because movement was only in one direction (i.e., into the study area), the abundance estimates are valid and germane to the second event. Brown and Daum's (2015) telemetry data indicated that some fish are still moving upstream into the study area during the period of the first sampling event but radiotagged fish completed upstream movements into the study area by the onset of the second sampling event. The magnitude of immigration is unknown but thought to be significant. In both years, while sampling the lowest section in the sampling area during the first event, field crews reported capturing most fish along cut-banks and the edges of the main channel (i.e., fish appeared to be actively moving upstream). This contrasted with much of the remaining study area where most fish were captured in shallower habitats along gravel and sand bars outside of the main river current (i.e., fish appeared to be staging for spawning).

The Bering cisco abundance estimates presented here are estimates of spawning abundance, which are a different component of the population than those harvested in the commercial fishery. In both years of this study, all female Bering cisco that were sampled had GSI values significantly >3%, confirming that they were sexually mature and preparing to spawn. Similarly, the GSI values collected from Bering cisco migrating upstream past Rapids (Figure 1) indicated that all were mature and preparing to spawn in the fall of the year they were collected (Brown et al. 2012b). In contrast, GSI values of all female Bering cisco sampled from the fall commercial fishery in the Yukon River delta in September 2009 and 2010 were <3%, indicating that those individuals would not spawn that year (L. DuBios, Commercial Fisheries Biologist, ADF&G, Anchorage, unpublished data). Although these, and future, spawning abundance estimates may be utilized for management of the commercial fishery, considerations must be made to distinguish the estimate of spawning abundance from the non-spawning population targeted by the commercial fishery.

Limited data is available documenting sex ratios in spawning Bering cisco populations. Both years of this study observed male-dominated sex ratios (64% and 74.5%). Sex composition of Bering cisco captured en route to spawning areas in the Susitna River showed male:female ratios of 1:1 (50% male) and 1.4:1 (58% male) in 1981 and 1982, respectively (ADF&G 1983). In contrast to the current study, Bering cisco sampled in 2009–2010 and 2012–2013 at Rapids on the Yukon River during their upstream migration to the Yukon Flats for spawning had relatively even or female dominated sex ratios (53–67% female; R. Brown, Fisheries Biologist, USF&WS, Fairbanks, unpublished data). However, those sampling efforts did not encompass the entire spawning migration in each of the 4 years and thus it is unknown if the observed sex ratios were representative of the entire population in any given year. Sampling of Bering cisco harvested in the 2015–2017 commercial fisheries at the mouth of the Yukon River reported similar sex ratios as those observed at Rapids (S. Garcia, Fishery Biologist, ADF&G, Anchorage, memorandums, December 2015 and October 2016; D. Jallen, Fishery Biologist, ADF&G, Anchorage, memorandum, November 2017). Although long-term (i.e., >20 years) Bering cisco data sets do not exist, an analysis of a similar data set for bloater *Coregonus hoyi* in Lake Michigan linked periods with female dominated sex ratios to poor recruitment (Bunnell et al. 2006). In the future, sex ratio analyses may represent a potential recruitment assessment method, but at this juncture, further directed research into this topic specific to Bering cisco would be required.

All common whitefish species present in the Yukon River drainage are known to be iteroparous (Alt 1969a; Mann 1974; Moulton et al. 1997; Brown 2004; Brown et al. 2012a). However, no specific evidence or observations of iteroparity have been reported for Bering cisco. Based upon evidence from this and other studies, at least some of the Bering cisco that spawn in the Upper Yukon Flats survive spawning and return to feeding and rearing areas. Over both years of this study, 4 fish marked in our study were recaptured in the Lower Yukon River by subsistence fishers in the year following marking (i.e., those individuals survived spawning and migrated back downstream to rearing and feeding areas). These recaptures, coupled with observations of residual eggs in 2 female fish that were collected for GSI sampling, indicated that each year a small proportion of the spawning Bering cisco survived post-spawning to return to feeding and rearing areas. These surviving fish may return to spawn again in later years. While comprising a small component of the overall number of fish sampled, fish aged 6–12 were present in the spawning population. Given that the minimum age of male and female spawning fish in this study was 3 years old, some, if not all, of the older individuals (>6–7 years old) observed likely survived to spawn more than once in their lifespans. This conclusion is supported by Brown and Daum (2015) who reported that 14 (17%) radiotagged Bering cisco that spawned in the Yukon Flats in fall 2012

were recorded migrating downstream past Rapids after spawning. In 2013, the same station recorded 58 fish (75%) making a similar post-spawning downstream migration. Additionally, age distribution data collected from harvests in the fall commercial fishery (2006–2015) indicated that fish with ages >6 accounted for 2–11% and 1–11% of the harvests for females and males, respectively (Andy Padilla, Fisheries Biologist, ADF&G, Fairbanks, memorandum, June 2015). These data indicate that Bering cisco are iteroparous and that a proportion of the spawning population, though assumed small, survive to spawn again.

RECOMMENDATIONS

Due to the annual commercial and subsistence fisheries that prosecute Bering cisco in the Yukon River and the recent commercial harvest quota increase from 25,000 to 35,000 fish, continued monitoring of this spawning population is recommended. Continued commercial harvest sampling as well as annual age, sex, and length sampling of the spawning population coupled with periodic (e.g., every 5–10 years) abundance estimates will assist with identifying fishery-related changes and natural fluctuations in abundance and population demographics. It is believed that >2,000 sex and length samples and >300 age samples can be collected in 4–5 days of sampling with one electrofishing boat (3 field personnel) during early October in the study area described here.

Future abundance estimates should follow this experiment's study design, which was successful and statistically sound. Although the timing of sampling events was not ideal due to significant immigration during the first event, sampling over the entire study area cannot be completed during a period where closure exists without significantly increasing the sampling effort and associated cost due to the onset of winter.

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APPENDIX A

Appendix A1.—Detection and mitigation of selective sampling during a two-event mark–recapture experiment.

Size- and sex-selective sampling may cause bias in two-event mark–recapture estimates of abundance and size and sex composition. Kolmogorov-Smirnov (KS) two-sample tests are used to detect size-selective sampling and contingency table analyses (Chi-square tests of independence) are used to detect evidence of sex-selective sampling.

Results of the KS and Chi-square tests will dictate whether the data needs to be stratified to obtain an unbiased estimate of abundance. The nature of the detected selectivity will also determine whether the first, second, or both event samples are used for estimating size and sex compositions.

DEFINITIONS

M = Lengths or sex of fish marked in the first event

C = Lengths or sex of fish inspected for marks in the second event

R = Lengths or sex of fish marked in the first event and recaptured in the second event

SIZE-SELECTIVE SAMPLING: KS TESTS

Three KS tests are used to test for size-selective sampling.

KS Test 1	C vs R	Used to detect size selectivity during the 1st sampling event. H ₀ : Length distributions of populations associated with C and R are equal
KS Test 2	M vs R	Used to detect size selectivity during the 2nd sampling event. H ₀ : Length distributions of populations associated with M and R are equal
KS Test 3	M vs C	Used to corroborate the results of the first two tests. H ₀ : Length distributions of populations associated with M and C are equal

SEX-SELECTIVE SAMPLING: CHI-SQUARE TESTS

Three contingency table analyses (χ^2 -tests on 2x2 tables) are used to test for sex-selective sampling.

χ^2 Test 1	C vs R	Used to detect sex selectivity during the 1st sampling event H ₀ : Sex is independent of the C - R classification
χ^2 Test 2	M vs R	Used to detect sex selectivity during the 2nd sampling event H ₀ : Sex is independent of the M - R classification
χ^2 Test 3	M vs C	Used to corroborate the results of the first two tests. H ₀ : Sex is independent of the M - C classification

Table A1-1 presents possible results of selectivity testing, their interpretation, and prescribed action.

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Table A1-1. Possible results of selectivity testing, interpretation, and action.

Case	KS or χ^2 Test						Interpretation and Action
	M (2nd event test)	vs. R	C (1st event test)	vs. R	M (1st vs 2nd event)	C	
I	Fail to reject H_0		Fail to reject H_0		Fail to reject H_0		Interpretation: No selectivity during either sampling event. Action: Abundance: Use a Petersen-type model without stratification. Composition: Use all data from both sampling events.
II	Reject H_0		Fail to reject H_0		Reject H_0		Interpretation: No selectivity during the 1st event but there is selectivity during the 2nd event. Action: Abundance: Use a Petersen-type model without stratification. Composition: Use data from the 1st sampling event without stratification. 2nd event data only used if stratification of the abundance estimate is performed, with weighting according to Equations 1–3 below.
III	Fail to reject H_0		Reject H_0		Reject H_0		Interpretation: No selectivity during the 2nd event but there is selectivity during the 1st event. Action: Abundance: Use a Petersen-type model without stratification. Composition: Use data from the 2nd sampling event without stratification. 1st event data may be incorporated into composition estimation only after stratification of the abundance estimate and appropriate weighting according to Equations 1–3 below.
IV	Reject H_0		Reject H_0		Either result		Interpretation: Selectivity during both 1st and 2nd events. Action: Abundance: Use a stratified Petersen-type model, with estimates calculated separately for each stratum. Sum stratum estimates for overall abundance. Composition: Combine stratum estimates according to Equations 1-3 below.
V	Fail to reject H_0		Fail to reject H_0		Reject H_0		Interpretation: The results of the 3 tests are inconsistent. Action: Need to determine which of Cases I-IV best fits the data. Inconsistency can arise from high power of the M vs. C test or low power of the tests involving R. Examine sample sizes (generally M or C from <100 fish and R from <30 are considered small), magnitude of the test statistics (D_{\max}), and the P -values of the three tests to determine which Cases I-IV best fits the data.

-continued-

COMPOSITION ESTIMATION FOR STRATIFIED ESTIMATES

An estimate of the proportion of the population in the k^{th} size or sex category for stratified data with I strata is calculated as follows:

$$\hat{p}_k = \sum_{i=1}^I \frac{\hat{N}_i}{\hat{N}} \hat{p}_{ik}, \quad (1)$$

with variance estimated as:

$$var[\hat{p}_k] \approx \frac{1}{\hat{N}^2} \sum_{i=1}^I \left(\hat{N}_i^2 var[\hat{p}_{ik}] + (\hat{p}_{ik} - \hat{p}_k)^2 var[\hat{N}_i] \right) \quad (2)$$

where:

$\hat{p}_{ik} =$	estimated proportion of fish belonging to category k in stratum i ;
$\hat{N}_i =$	estimated abundance in stratum i ; and
$\hat{N} =$	estimated total abundance $= \sum_{i=1}^I \hat{N}_i$

TESTS OF CONSISTENCY FOR PETERSEN ESTIMATOR

Three contingency table analyses are used to determine if the Petersen estimator can be used (Seber 1982). If any of the null hypotheses are not rejected, then a Petersen estimator may be used. If all three of the null hypotheses are rejected, a temporally or spatially-stratified estimator (Darroch 1961) should be used to estimate abundance.

Seber (1982) describes 4 conditions that lead to an unbiased Petersen estimate, some of which can be tested directly:

1. Marked fish mix completely with unmarked fish between events.
2. Equal probability of capture in event 1 and equal movement patterns of marked and unmarked fish.
3. Equal probability of capture in event 2.
4. The expected number of marked fish in recapture strata is proportional to the number of unmarked fish.

In the following tables, the terminology of Seber (1982) is followed, where a represents fish marked in the first event, n fish captured in second event and m marked fish recaptured; $m_{.j}$ and $m_{i.}$ represent summation over the i^{th} and j^{th} indices, respectively.

I. Mixing Test

Tests the hypothesis (condition 1) that movement probabilities (θ_{ij}), describing the probability that a fish moves from marking stratum i to recapture stratum j , are independent of marking stratum: $H_0: \theta_{ij} = \theta_j$ for all i and j .

Area/Time Marking Strata (i)	Area/Time Recapture Strata (j)				Not Recaptured $a_i - m_{i.}$
	1	2	...	t	
1	m_{11}	m_{12}	...	m_{1t}	$a_1 - m_{1.}$
2	m_{21}	m_{22}	...	m_{2t}	$a_2 - m_{2.}$
...
s	m_{s1}	m_{s2}	...	m_{st}	$a_s - m_{s.}$

II. Equal Proportions Test^a (SPAS^b terminology)

Tests the hypothesis (condition 4) that the marked to unmarked ratio among recapture strata is constant: $H_0: \sum_i a_i \theta_{ij} / U_j = k$, where $k = \text{a constant}$, $U_j = \text{unmarked fish in stratum } j \text{ at the time of } 2^{\text{nd}} \text{ event sampling}$, and $a_i = \text{number of marked fish released in stratum } i$. Failure to reject H_0 means the Petersen estimator should be used only if the degree of closure among tagging strata is constant, i.e. $\sum_j \theta_{ij} = \lambda$ (Schwarz and Taylor 1998; p 289). A special case of closure is when all recapture strata are sampled, such as in a fishwheel to fishwheel experiment, where $\sum_j \theta_{ij} = 1.0$; otherwise biological and experimental design information should be used to assess the degree of closure.

	Area/Time Recapture Strata (j)			
	1	2	...	t
Marked ($m_{.j}$)	$m_{.1}$	$m_{.2}$...	$m_{.t}$
Unmarked ($n_j - m_{.j}$)	$n_1 - m_{.1}$	$n_2 - m_{.2}$...	$n_t - m_{.t}$

-continued-

III. Complete Mixing Test^a (SPAS^b terminology)

Tests the hypothesis that the probability of re-sighting a released animal is independent of its stratum of origin: $H_0: \sum_j \theta_{ij} p_j = d$, where p_j is the probability of capturing a fish in recapture stratum j during the second event, and d is a constant.

	Area/Time Marking Strata (i)			
	1	2	...	s
Recaptured (m_i)	$m_{1\bullet}$	$m_{2\bullet}$...	$m_{s\bullet}$
Not Recaptured ($a_i - m_{i\bullet}$)	$a_1 - m_{1\bullet}$	$a_2 - m_{2\bullet}$...	$a_s - m_{s\bullet}$

^a There is no 1:1 correspondence between Tests II and III and conditions 2-3 above. It is pointed out that equal probability of capture in event 1 will lead to (expected) non-significant Test II results, as will mixing, and that equal probability of capture in event 2 along with equal closure ($\sum_j \theta_{ij} = \lambda$) will also lead to (expected) non-significant Test III results.

^b Stratified Population Analysis System (Arnason, A. N., C. W. Kirby, C. J. Schwarz, and J. R. Irvine. 1996. Computer Analysis of Data from Stratified Mark-Recovery Experiments for Estimation of Salmon Escapements and Other Populations, Canadian Technical Report of Fisheries and Aquatic Sciences 2106)

APPENDIX B

Appendix B1.—Capture history by river section of all Bering cisco examined in 2016.

	Section recaptured										m_2^a	n_1	m_2/n_1^b
	A	B	C	D	E	F	G	H	I	J			
A	0	0	0	0	0	0	0	0	0	0	0	84	0.0
B	0	2	1	0	0	0	0	0	0	0	3	220	0.014
C	2	0	4	0	0	0	0	0	0	0	6	326	0.018
D	0	2	2	4	0	0	0	0	0	0	8	318	0.025
E	2	2	1	2	6	2	0	0	0	0	15	636	0.024
F	0	2	3	5	3	3	1	0	0	0	17	447	0.038
G	0	1	3	2	3	4	3	3	0	0	19	886	0.021
H	0	0	0	0	1	1	5	2	0	0	9	898	0.010
I	0	0	0	0	2	1	5	3	3	0	14	523	0.027
J	0	0	0	0	0	1	1	5	5	1	13	699	0.019
m_2^a	4	9	14	13	15	12	15	13	8	1			
n_2	433	536	731	553	817	974	1129	1306	894	777			
m_2/n_2^c	0.009	0.017	0.019	0.024	0.018	0.012	0.013	0.010	0.009	0.001			

^a Total number of recaptured marked fish (m_2) was 105; however, one recaptured fish had lost its tag and as such could not be attributed to a sampling section.

^b Probability of capture during the first event.

^c Probability of capture during the second event.

Appendix B2.—Capture history by river section of all Bering cisco examined in 2017.

	Section recaptured										m ₂	n ₁	m ₂ / n ₁ ^a
	A	B	C	D	E	F	G	H	I	J			
Section marked	A	2	0	0	0	0	0	0	0	0	2	648	0.003
	B	2	0	0	1	0	0	0	0	0	3	213	0.014
	C	3	4	3	0	1	0	0	0	0	11	408	0.027
	D	0	3	3	1	1	0	0	1	0	9	664	0.014
	E	0	2	5	1	2	2	0	0	0	12	422	0.028
	F	0	1	0	1	1	1	0	0	1	5	200	0.025
	G	0	0	0	0	3	3	8	1	0	15	476	0.032
	H	1	1	4	0	1	3	12	17	2	41	917	0.048
	I	0	0	0	1	1	0	5	8	4	19	624	0.030
	J	0	0	1	0	0	1	1	6	4	14	461	0.030
m ₂	8	11	16	5	10	10	26	33	10	2			
n ₂	717	595	1014	925	787	748	1585	1771	1106	906			
m ₂ / n ₂ ^b	0.011	0.018	0.016	0.005	0.013	0.013	0.016	0.019	0.009	0.002			

^a Probability of capture during the first event.

^b Probability of capture during the second event.

APPENDIX C

Appendix C1.–Petersen mark–recapture abundance estimation model when the upstream boundary is open.

The following text describes the Petersen mark–recapture model used in the Upper Yukon Flats Bering cisco spawning abundance study assuming (only) the upper study boundary is open to emigration. The estimator is based on mark–recapture data collected over 10 subsections of river of equal length. This appendix relies heavily on Evenson (1988).

Estimation of upstream movement

Three contiguous sections were created from the 10 subsections of the study as follows:

	Subsection	1	2	3	4	5	6	7	8	9	10	
Downstream	Section	Not Used	1			2			3			Upstream

The following notation is used in the estimation of θ_U :

- θ_U = Probability a fish moves out of a section in the upstream direction.
- M_x = Number of fish marked in the 1st event in section x ($x=1, 2$, or 3 for the downstream, midstream and upstream sections, respectively).
- m_x = Number of fish marked in section x ($x = 1, 2$, or 3) in the 1st event **AND** that remain in one of the 3 sections at the start of the 2nd event.
- R_{xy} = Number of fish that were marked in section x ($x = 1, 2$, or 3) in the 1st event **AND** were recaptured in section y ($y=1, 2$, or 3) in the 2nd event.
- $R_{..}$ = Number of recaptures in the 2nd event from sections 1, 2, or 3
- $R_{2.}$ = Number of recaptures in the 2nd event of fish tagged in section 2, the midstream section.
- p = Probability a fish is caught in the 2nd event.
- Φ_u = Probability a fish moves out of a section in the upstream direction **AND** is caught in the 2nd event (note that $\Phi_u = p \theta_U$).

The probability of movement, θ_U , can be estimated with information on recaptured fish among the sections. The probability of recapturing R_{12} and R_{23} marked fish upstream from where they were released is given by the joint probability density function (PDF):

$$P(R_{12}, R_{23}) = P(R_{12})P(R_{23}) = \binom{M_1}{R_{12}} \phi_U^{R_{12}} (1 - \phi_U)^{M_1 - R_{12}} \binom{M_2}{R_{23}} \phi_U^{R_{23}} (1 - \phi_U)^{M_2 - R_{23}} \quad (1)$$

Note that Φ_u is presumed to be the same for the transition from section 1 to 2 and from section 2 to 3, which can only be so when sections 1 and 2 are the same size **and** when the probability of capture in the 2nd event is the same for all fish throughout the study area. The assumption that the third section is the same size as 1 and 2 is used in the estimation of m_3 (Equation 9).

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An estimate of Φ_u is given by its MLE:

$$\hat{\phi}_U = \frac{R_{12} + R_{23}}{M_1 + M_2} \quad (2)$$

From the relationship $\Phi_u = p \theta_U$, an estimate of θ_U is therefore:

$$\hat{\theta}_U = \frac{\frac{R_{12} + R_{23}}{M_1 + M_2}}{\hat{p}} \quad (3)$$

The PDF(R_2) is used to obtain \hat{p} :

$$P(R_2) = \binom{M_2}{R_2} p^{R_2} (1-p)^{M_2 - R_2} \quad (4)$$

An estimate of p is given by its MLE: $\frac{R_2}{M_2}$, which when substituted into Eq 3 gives:

$$\hat{\theta}_U = \frac{M_2(R_{12} + R_{23})}{R_2(M_1 + M_2)} \quad (5)$$

A second estimate of θ_U could be obtained using subsections 1–9, in a manner identical to that described in Equations 1–5; an average of the two estimates of θ_U would then be calculated. A second estimate was not calculated for this study given only one subsection out of 10 subsections was omitted in the estimation of θ_U described above.

Estimation of Abundance

Adding the most-downstream subsection (1) to the analysis, we introduced another section (1') as follows:

	Subsection	1	2	3	4	5	6	7	8	9	10	
Downstream	Section	1'	1			2			3			Upstream

The following additional notation is used in the estimation of abundance:

- C = Number of fish sampled in the 2nd event (sections 1', 1, 2, 3).
- R'.. = Number of recaptures in the 2nd event from (sections 1', 1, 2, 3)
- N = Abundance of fish in entire study area (sections 1', 1, 2, 3) at the start of the 2nd event.

With respect to the number of marked fish available for recapture at the start of the 2nd event, only m_3 is stochastic because fish tagged in sections 1', 1 and 2 are presumed unable to move far enough upstream to leave the study area and so $m_{1'} = M_{1'}$, $m_1 = M_1$, and $m_2 = M_2$. The joint PDF for the number of marked fish recaptured during the 2nd event ($R'_{..}$) and m_3 is:

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$$P(R'_{..}, m_3) = \binom{C}{R'_{..}} \left[\frac{M_{1'} + M_1 + M_2 + m_3}{N} \right]^{R'_{..}} \left[1 - \frac{M_{1'} + M_1 + M_2 + m_3}{N} \right]^{C-R'_{..}} * \binom{M_3}{m_3} (1 - \theta_U)^{m_3} \theta_U^{M_3 - m_3} \quad (6)$$

where $M_{1'} + M_1 + M_2 + m_3$ is the number of marked fish still in the study area at the start of the 2nd event. The likelihood for N is:

$$L(N) = \left[\frac{M_{1'} + M_1 + M_2 + m_3}{N} \right]^{R'_{..}} \left[1 - \frac{M_{1'} + M_1 + M_2 + m_3}{N} \right]^{C-R'_{..}} K \quad (7)$$

where K collects terms not involving N .

The MLE(N) is then:

$$\hat{N} = \frac{C(M_{1'} + M_1 + M_2 + m_3)}{R'_{..}} \quad (8)$$

To calculate \hat{N} , an estimate of m_3 is therefore required. The PDF of m_3 is:

$$P(m_3) = \binom{M_3}{m_3} (1 - \theta_U)^{m_3} \theta_U^{M_3 - m_3} \quad (9)$$

such that

$$\hat{m}_3 = M_3(1 - \theta_U) \quad (10)$$

Using estimates for θ_U (Eq 5) and m_3 (Eq 10) the abundance is estimated as:

$$\hat{N} = \frac{(C+1) \left[M_{1'} + M_1 + M_2 + M_3 \left[1 - \frac{M_2(R_{12} + R_{23})}{R_2(M_1 + M_2)} \right] \right]}{(R'_{..} + 1)} \quad (11)$$

The quantities $(C+1)$ and $(R'_{..}+1)$ are substituted for C and $R'_{..}$, respectively, to correct the bias in the binomial approximation of the hypergeometric probability distribution of the recaptures (Bailey 1951, 1952). The standard error of \hat{N} was calculated using resampling techniques as described in Efron (1982).