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Abundance and Spawning Distribution of Susitna River Chum *Oncorhynchus keta* and Coho *O. kisutch* Salmon, 2012

by

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Alaska Department of Fish and Game **Divisions of Sport Fish and Commercial Fisheries**

Symbols and Abbreviations

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Weights and measures (metric)

centimeter	cm
deciliter	dL
gram	g
hectare	ha
kilogram	kg
kilometer	km
liter	L
meter	m
milliliter	mL
millimeter	mm

Weights and measures (English)

cubic feet per second	ft^3/s
foot	ft
gallon	gal
inch	in
mile	mi
nautical mile	nmi
ounce	oz
pound	lb
quart	qt
yard	yd

Time and temperature

day	d
degrees Celsius	°C
degrees Fahrenheit	°F
degrees kelvin	K
hour	h
minute	min
second	s

Physics and chemistry

all atomic symbols	
alternating current	AC
ampere	A
calorie	cal
direct current	DC
hertz	Hz
horsepower	hp
hydrogen ion activity (negative log of)	pH
parts per million	ppm
parts per thousand	ppt, ‰
volts	V
watts	W

General

Alaska Administrative Code	AAC
all commonly accepted abbreviations	e.g., Mr., Mrs., AM, PM, etc.
all commonly accepted professional titles	e.g., Dr., Ph.D., R.N., etc.
at	@
compass directions:	
east	E
north	N
south	S
west	W
copyright	©
corporate suffixes:	
Company	Co.
Corporation	Corp.
Incorporated	Inc.
Limited	Ltd.
District of Columbia	D.C.
et alii (and others)	et al.
et cetera (and so forth)	etc.
exempli gratia (for example)	e.g.
Federal Information Code	FIC
id est (that is)	i.e.
latitude or longitude	lat or long
monetary symbols (U.S.)	$, ¢
months (tables and figures): first three letters	Jan,...,Dec
registered trademark	®
trademark	™
United States (adjective)	U.S.
United States of America (noun)	USA
U.S.C.	United States Code
U.S. state	use two-letter abbreviations (e.g., AK, WA)

Mathematics, statistics

all standard mathematical signs, symbols and abbreviations	
alternate hypothesis	H_A
base of natural logarithm	*e*
catch per unit effort	CPUE
coefficient of variation	CV
common test statistics	(F, t, χ^2, etc.)
confidence interval	CI
correlation coefficient (multiple)	R
correlation coefficient (simple)	r
covariance	cov
degree (angular)	°
degrees of freedom	df
expected value	*E*
greater than	>
greater than or equal to	≥
harvest per unit effort	HPUE
less than	<
less than or equal to	≤
logarithm (natural)	ln
logarithm (base 10)	log
logarithm (specify base)	log_2, etc.
minute (angular)	'
not significant	NS
null hypothesis	H_O
percent	%
probability	P
probability of a type I error (rejection of the null hypothesis when true)	α
probability of a type II error (acceptance of the null hypothesis when false)	β
second (angular)	"
standard deviation	SD
standard error	SE
variance	
population	Var
sample	var

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure **Page**

LIST OF APPENDICES

Appendix **Page**

ABSTRACT

In 2009, the Alaska Department of Fish and Game began a 4-year spawning distribution and abundance estimation study in response to concerns over the status of the Susitna River chum (*Oncorhynchus keta*) and coho (*O. kisutch*) salmon stocks. This report summarizes results of mark–recapture abundance and distribution assessments completed during 2012. Four fish wheels were used at river mile (RM) 22 in the Susitna River to capture and tag chum and coho salmon with dart tags in July and August 2012. Two fish wheels were used at RM 6 in the Yentna River and 2 fish wheels were used at RM 34 in the mainstem Susitna River to sample salmon for tags. Estimated spawning abundance of chum salmon was 229,903 (SE 155,193) fish for the mainstem Susitna River and 99,442 (SE 84,876) fish for the Yentna River. Estimated spawning abundance of coho salmon was 90,397 (SE 36,701) fish for the mainstem Susitna River and 93,919 (SE 10,688) fish for the Yentna River. A total of 799 radio tags were placed in chum and coho salmon. Their movements were tracked using 10 ground tracking stations, 15 aerial surveys of the mainstem Susitna River, 6 aerial surveys of the Yentna River, and 2 drainagewide aerial surveys. All but 50 of the radio tags were relocated, and 716 (89.6%) were assigned a putative spawning location. Both chum and coho salmon exhibited bank orientation at the tagging site.

Key words: chum salmon, coho salmon, abundance, mark–recapture, Susitna River, Yentna River, spawning distribution, fish wheel, radio telemetry

INTRODUCTION

The Susitna River chum (*Oncorhynchus keta*) and coho (*O. kisutch*) salmon stocks contribute to commercial and sport harvests in upper Cook Inlet (UCI). The 1966–2012 average commercial harvest in UCI was 442,207 chum salmon and 297,372 coho salmon (Shields and Dupuis 2013). Annual sport harvests from the Susitna River averaged 2,555 chum and 36,228 coho salmon from 1998 to 2012 (calculated from tables in Oslund et al. 2013).

From 1981 through 1985, fishery studies were conducted for a proposed Susitna River hydroelectric project. To estimate abundance, chum and coho salmon data were collected from the Yentna River at river mile (RM) 6.2 (Yentna Site) from 1981 through 1984, at the Sunshine Site (RM 80 of the Susitna River) from 1981 through 1985, and at the Flathorn Site (RM 22 of the Susitna River) in 1984 and 1985. With the exception of the Yentna Site, which used sonar, all other estimates were generated using mark–recapture techniques. The 1981–1985 average chum salmon abundance estimate for fish that migrated upstream of the Sunshine Site was 419,540; for the Yentna Site, the 1981–1984 estimated average was 21,225 chum salmon; and for the Flathorn Site, the 1984–1985 estimated average was 564,750 chum salmon. Average coho salmon estimates for the same years were 19,500 fish at the Yentna Site, 42,440 fish at the Sunshine Site, and 133,750 fish at the Flathorn Site (Barrett et al. 1985; Thompson et al. 1986).

In 1981, the first radiotagging study was conducted when 11 chum and 10 coho salmon were radiotagged at Talkeetna (RM 103) and at Curry (RM 120) (ADF&G 1981). In 2002, a Susitna River drainagewide coho salmon estimate of 663,000 fish was generated using mark–recapture techniques (Willette et al. 2003). During that study, 179 coho salmon were radiotagged in Cook Inlet and tracked to the Susitna River drainage. Results of this study provided the first drainagewide spawning distribution information for coho salmon.

User groups have been concerned over the status of coho and chum salmon stocks in the Susitna River and have brought the issue before the Alaska Board of Fisheries (BOF). At the 2008 BOF meeting, there were 69 proposals to modify commercial fishing regulations in UCI and 2 proposals for sport fishing regulations in the Susitna River, demonstrating the importance of the fisheries. In addition, the BOF issued resolution 2008-253-FB to the Alaska Legislature supporting funding for fisheries research. The Matanuska–Susitna Borough issued a resolution on 15 January 2008 requesting the Alaska Department of Fish and Game (ADF&G) declare Susitna River chum salmon a "stock of concern," enumerate salmon escapements, and set escapement goals for all salmon in northern Cook Inlet. The Alaska State Legislature issued Legislative Resolve Number 51 in 2008 establishing the Cook Inlet Salmon Task Force to examine "conservation and allocation issues."

In 2009, ADF&G initiated a 4-year spawning distribution study (2009–2012) using radio telemetry. In 2010, ADF&G added an abundance estimation component. The objectives for 2012 were to use mark–recapture techniques and radiotagging to 1) estimate inriver abundance of adult chum and coho salmon above the Flathorn Site, 2) identify chum and coho salmon spawning locations throughout the Susitna River drainage by fishwheel tagging site, and 3) estimate the proportions of chum and coho salmon spawning in 15 major tributaries (or groupings of minor tributaries).

STUDY AREA

The Susitna River watershed, the fourth largest drainage in the state of Alaska, is 49,210 km^2 and originates in the Alaska Range north of Anchorage (Figure 1). The Susitna River flows generally south from the Alaska Range for approximately 400 km before entering UCI west of Anchorage. Some tributaries that originate in the Alaska or Talkeetna mountain ranges have clear water whereas others are glacially turbid (Sweet et al. 2003). The largest tributaries are the Yentna, Chulitna, and Talkeetna rivers, and numerous small lakes (King and Walker 1997).

METHODS

ABUNDANCE

Abundances of chum and coho salmon were estimated using 2-sample mark–recapture techniques.

Marking Events

Four fish wheels were operated in 2012 at the Flathorn Site (RM 22 Susitna River): 1 on each bank and 2 on islands in the Susitna River (Figure 2). These sites were selected because they are upstream of a highly braided area and downstream of the confluence with the Yentna River. Picket weirs were installed between each fish wheel and the river bank to direct migrating salmon away from the bank and towards the fish wheel baskets.

The 4 fish wheels (FWs 1–4) were operated from 6 July through 26 August 2012, and all healthy chum and coho salmon were marked with dart tags, and a subsample were marked with radio tags, which were subsequently tracked to spawning locations. During 6 July through 14 August, the Division of Commercial Fisheries (CF) used FW 1 as part of a fish wheel selectivity study, when all captured sockeye (*O. nerka*) and pink (*O. gorbuscha*) salmon, in addition to chum and coho salmon, were marked with an external tag, and a subsample of fish were each marked with a radio tag and subsequently tracked to spawning locations (Willette et al. 2016).

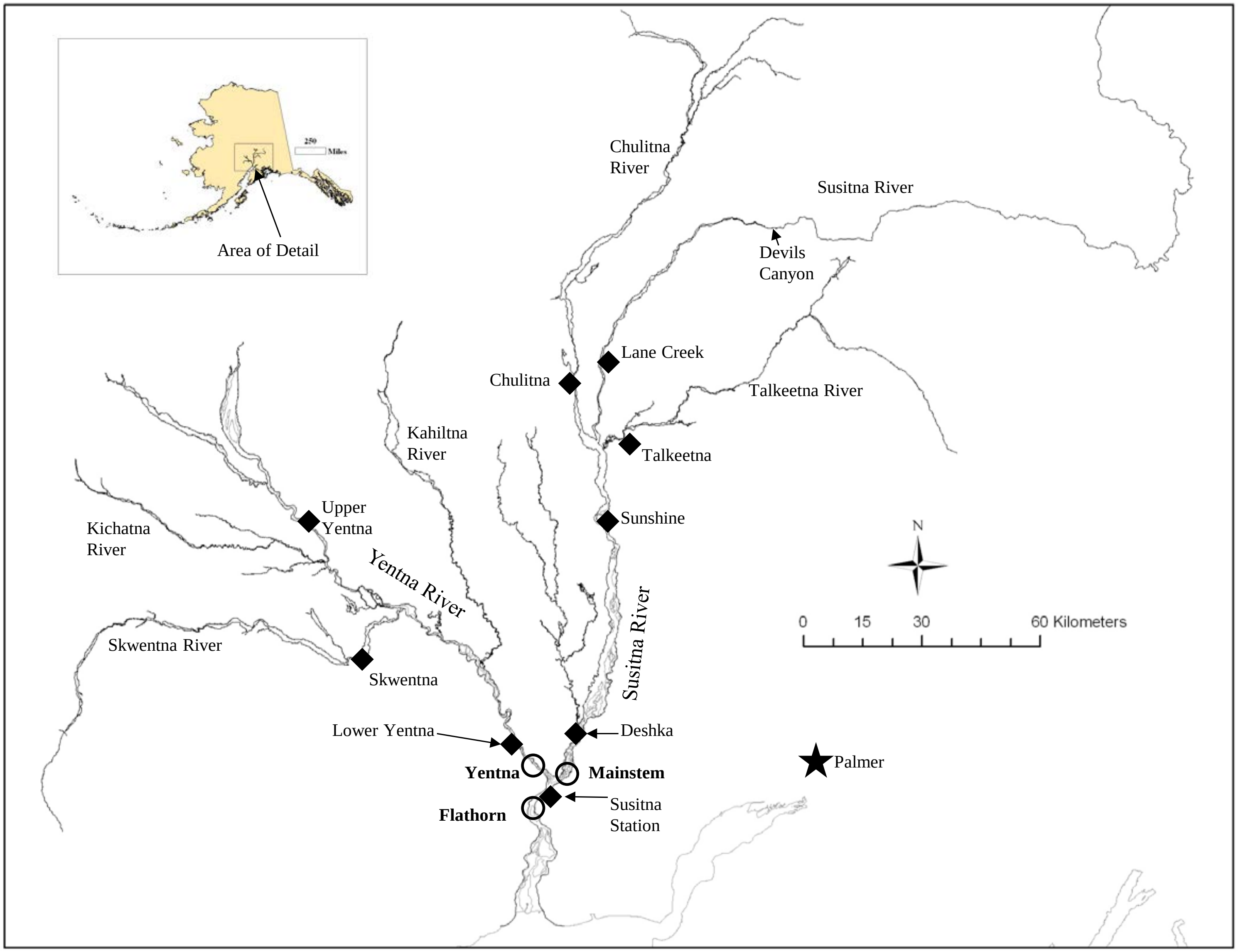

Figure 1.–Locations of Flathorn, Mainstem, and Yentna fish wheel sites (circles) and fixed radiotracking stations (diamonds) in the Susitna River drainage, 2012.

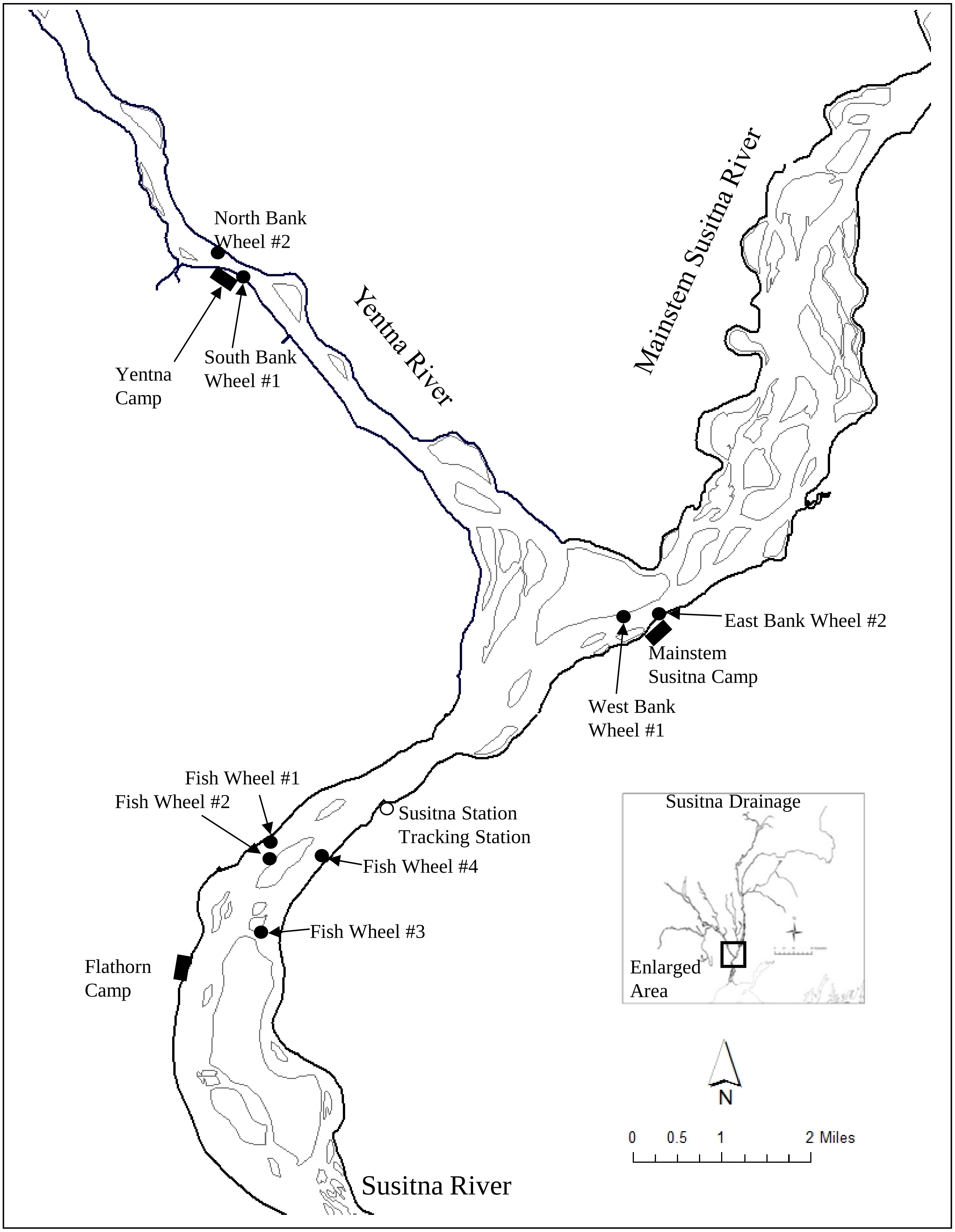

Figure 2.–Locations of Flathorn, Mainstem, and Yentna fish wheels (circles); Flathorn, Mainstem, and Yentna field camps (rectangles); and a radiotracking station (open circle) during 2012.

Division of Sport Fish (SF) crews, working at least two 7.5-hour shifts each day, operated FWs 2–4 during daylight hours until reaching the goal of 12 h/d of effort per fish wheel. CF crews, working two 9-hour shifts each day, operated FW 1 until reaching the goal of 18 h/d of effort because more tagged fish were needed for the CF selectivity study. Effort at FW 1 was reduced to 12 h/d when the SF crew replaced the CF crew on 14 August. All fish wheels were operated each day except when repairs were needed or high water events occurred.

Fish wheels were constructed of aluminum, with two 6.5 ft x 6.6 ft baskets webbed with knotted nylon 1.5-inch (square measure) mesh. Captured fish descended the basket chute and exited via an aluminum-framed fabric "slide" and dropped into a live box. Live boxes measured 8 ft long, 2 ft wide, and 3 ft deep, with plywood sides with holes for water circulation. The configuration of the fish wheel axle, baskets, and floats allowed the baskets to reach a maximum depth of 4.5 ft. Fish wheels were secured to the riverbank and held offshore with poles to reach sufficient current and depth to spin the baskets. The axle height was adjusted so that the baskets swept as close to the river bottom as possible.

At the Flathorn Site, all captured chum and coho salmon at least 400 mm from mid eye to tail fork (METF) and in good condition were marked with an individually numbered, yellow, 6-inch-long dart tag (either model FT-1-94 from Floy Tag, Seattle, WA, or model PDA from Hallprint, Australia[1]). All tagged fish were measured for METF length. At FWs 2–4, the adipose fin was removed from dart-tagged salmon as a secondary mark to detect tag loss. At FW 1, no secondary mark was used. The CF selectivity study at FW 1 tagged 4 species of salmon and required that all species be treated identically; additional handling, such as removing the adipose fin from only chum and coho salmon, might have introduced additional handling effects. Also, the crews at the Yentna recovery site were expected to handle many thousands of fish of all species, precluding accurate inspection of fish for a missing adipose fin.

Recapture Events

Yentna River

Two fish wheels were operated by CF on the Yentna River at RM 6.2 (Yentna Site) as part of an annual sonar project. The fish wheels were similar to the Flathorn Site fish wheels with a maximum fishing depth of 4.5 ft. For tag recovery, the fish wheels were operated from 7 July through 30 August from 0400 to 0830 hours, 0930 to 1400 hours, 1400 to 1830 hours, and 1930 to 2400 hours daily, for a total effort of 18 h/d/fish wheel. All captured fish were identified, counted, recorded, and inspected for the presence of a yellow dart tag; tag numbers were recorded.

Mainstem Susitna River

At the mainstem Susitna River recapture site (RM 34; Mainstem Site), 2 fish wheels were operated by SF for 12 h/d each (6 h/shift for 2 shifts). The fish wheels were similar in construction to those at the Flathorn Site. All captured fish were counted, recorded, and inspected for the presence of a yellow dart tag. Additionally, all chum and coho salmon were examined for an adipose fin to document tag loss. Tag numbers were recorded from recaptured salmon and the numbered end of the tag was removed and saved. Length data were collected

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1 Product names used in this publication are included for completeness but do not constitute product endorsement.

daily from the first 3 of each untagged chum and coho salmon captured at each wheel by each shift.

Abundance Estimation

Mark–recapture experiments were designed so that Chapman's modification to the Petersen estimator (Chapman 1951) could be used to estimate abundance of chum or coho salmon passing the Flathorn tagging site. For these estimates of abundance to be unbiased, certain assumptions must be met (Seber 1982). These assumptions, expressed in the circumstances of this study, along with their respective design considerations and test procedures were as follows:

1) Assumption I—the population is closed to births, deaths, immigration, and emigration.

   Considering the short distance between the first event site at Flathorn and the 2 second-event sampling sites just upstream, and the life history of these species, there should have been no recruitment between sampling events. First event sampling (marking) began prior to any significant passage of fish past the tagging sites and continued until run passage dropped to near zero.

   It was anticipated that some salmon, particularly coho salmon, might travel upstream to the Flathorn Site and be vulnerable to tagging but later spawn in tributaries below the Flathorn Site. The subsample of chum and coho salmon captured at the fish wheels and instrumented with radio tags was tracked and used to estimate the proportions of each species exhibiting this type of behavior, which was then used to adjust the number of valid marks downward appropriately.

2) Assumption II—there is no trap-induced behavior.

   There is no explicit test for this assumption because the behavior of unhandled fish cannot be observed. We attempted to meet this assumption by minimizing holding and handling time of all captured fish. Any obviously stressed or injured fish were not tagged. Examples of stress include fresh seal bites or other scars that penetrated into the muscle, capture injuries such as torn opercula or broken snouts, or being dropped in the boat while handling.

   Also, the subsample of chum and coho salmon instrumented with radio tags and then tracked was used to estimate handling mortality, specifically the proportion of fish marked at each wheel that failed to continue upstream after being handled and were not found in tributaries below the Flathorn Site.

3) Assumption III—tagged fish do not lose their marks between sampling events and all marks are recognizable.

   We attempted to estimate tag loss for only part of the abundance experiments. For reasons described in the methods, fish tagged with darts in the CF fish wheel selectivity study did not receive a secondary mark. However, the adipose fin of dart-tagged fish from FWs 2, 3, and 4 was removed for a secondary mark. Only chum and coho salmon captured at the Mainstem Site were examined for the presence of an adipose fin.

4) Assumption IV—at least 1 of the following 3 conditions must be met:

    1) All chum and coho salmon have the same probability of being caught in the first event.
    2) All chum and coho salmon have the same probability of being captured in the second event.
    3) Marked fish mix completely with unmarked fish between samples.

In these experiments, there was no expectation that marked and unmarked fish mixed completely. Fish wheels were operated continuously during the run; however, probabilities of capture of both chum and coho salmon were expected to vary as their migration progressed. For example, fluctuations in water levels at both first and second event sampling sites can affect the efficiency of fish wheels, resulting in variation in probability of capture over time. Also, the probabilities of capture were expected to vary between fish wheel sites during both first and second events due to differences in channel morphology and water flow (Yanusz et al. 2007).

Equal probability of capture was evaluated by time, area, and length of fish. The procedures for analyzing length data for statistical bias due to gear selectivity are described in Appendix A1. Size-biased sampling was not detected during either the first or second sampling events for both chum and coho salmon and therefore stratification was not necessary.

Contingency table analyses recommended by Seber (1982) and described in Appendix A2 were used to detect significant temporal or geographic violations of assumptions of equal probability of capture. The test for complete mixing (Test I in Appendix A2) was not performed. We assumed the complete mixing condition was violated geographically because of a strong tendency for bank orientation by chum and coho salmon at the Flathorn tagging site. This was demonstrated during the 2009 radiotelemetry study (Merizon et al. 2010), the 2010 mark–recapture experiments (Cleary et al. 2013), and in the 2012 data presented here. The complete mixing condition cannot be satisfied temporally due to experimental design and the timing of movements of fish being investigated.

Abundances for both chum and coho salmon were estimated using the model developed by Darroch (1961) because temporal or geographic heterogeneity in probability of capture was detected during both sampling events. The contingency tables described in Appendix A2 were also analyzed to identify 1) first-event strata (individual or contiguous groupings of temporal or geographic categories) where probability of recapture during the second event was homogeneous within strata and different between strata, and 2) second-event strata where ratios of marked to unmarked fish were homogeneous within strata and different between strata. Temporal categories comprised groupings of sample data collected by week, and geographic categories comprised fish wheel sites.

Prior to estimating abundance, it was necessary to adjust the number of marks deployed to account for fish lost due to handling as well as for fish that were not part of the populations being investigated (i.e., those that were vulnerable to capture at the Flathorn Site but spawned below that tagging site). Fates of radiotagged fish were used to estimate losses of marked fish from the experiments. For each first-event geographical and temporal (G-T) stratum, the number of valid marks entering the experiment was estimated as follows:

$$\hat{M}_s = M_{(\mathrm{Rel})s}\,\hat{p}_s \qquad (1)$$

where

$\hat{p}_s$ = the estimated proportion of valid marks in G-T stratum *s*, and

$M_{(\text{Rel})s}$ = the number of marked fish released ($_{\text{Rel}}$) in each first-event G-T stratum *s*.

Fates of radiotagged fish were used to estimate the following:

$$\hat{p}_s = \frac{n_{(\text{Sp})s}}{n_s} \tag{2}$$

where

n_s = the number of radiotagged fish released in G-T stratum *s*, and

$n_{(\text{Sp})s}$ = those fish in n_s that traveled upstream from the marking site to a spawning area ($_{\text{Sp}}$).

During both the chum and coho salmon mark–recapture experiments, data were lost for a few recaptured fish. Specifically, the dart tag number of these marked fish was not recorded or was recorded incorrectly. For these particular fish, if they were detected during second-event sampling, the site and date were recorded so that the second-event G-T stratum (*t*) was known for each of these fish. However, information was not available to identify the fish wheel and date where these recaptures were marked.

Within each second-event G-T stratum *t*, the probabilities that recaptured fish were marked in each of the *s* first-event G-T strata were estimated using the counts of recaptures with complete data:

$$\hat{p}_{(t)s} = \frac{r_{(k)s,t}}{r_{(k)\bullet,t}} \tag{3}$$

where

$r_{(k)s,t}$ = the number of recaptures with complete data that were known ($_k$) to have been marked in stratum *s* and recaptured in stratum *t*,

and where

$$r_{(k)\bullet,t} = \sum_{i=1}^{s} r_{(k)i,t} \ . \tag{4}$$

The total number of recaptures marked in first-event stratum *s* and recaptured in second-event stratum *t* was estimated as follows:

$$\hat{r}_{s,t} = r_{(k)s,t} + r_{(Unk)t}\,\hat{p}_{(t)s} \tag{5}$$

where

$r_{(Unk)t}$ = the number of recaptures with incomplete data ($_{Unk}$) known to have been recaptured in stratum *t*.

Initial modeling was conducted using the computer program SPAS (Arnason et al. 1996) after rounding $\hat{M}_s$ and $\hat{r}_{s,t}$ values to the nearest integers. For chum salmon, an admissible model was identified that contained 5 first-event strata and 5 second-event strata. For coho salmon, an admissible model was identified that contained 6 first-event strata and 6 second-event strata.

These “square” models allowed for computation of an analytical solution using matrix algebra described in Seber (1982). Actual values for $\hat{M}_s$ and $\hat{r}_{s,t}$ were used in the analytical model to provide estimates of abundance for both chum and coho salmon.

Variances and 95% confidence intervals for abundance estimates were estimated using bootstrap methods (Efron and Tibshirani 1993). For each bootstrap realization, recaptures with complete information were modeled as a multinomial process within first-event stratum *s* with parameters ($M_{(Rel),s}$, $\hat{p}_{(s)1}, \ldots \hat{p}_{(s)t}$, $\hat{p}_{(s)nr}$) where

$$\hat{p}_{(s)i} = \frac{r_{(k)s,i}}{M_{(\mathrm{Rel})s}} \tag{6}$$

for i = 1 to t, and

$$\hat{p}_{(s)nr} = 1.0 - \sum_{i=1}^{t} \hat{p}_{(s)i} \,. \tag{7}$$

Bootstrap variability in the process described in Equations 1 and 2 was modeled as a binomial processes with parameters (n_s, $\hat{p}_s$). Bootstrap variability in the process described in Equations 3–5 was modeled as a multinomial processes with parameters ($r_{(k)\bullet,t}$, $\hat{p}_{(t)1}, \ldots \hat{p}_{(t)s}$).

For each bootstrap realization, the analytical s × t Darroch (1961) model was then used to generate an estimate of abundance for that bootstrap realization. One million bootstrap realizations were generated for each experiment. The standard error for each parameter estimate was calculated as the standard deviation of the bootstrap distribution for that parameter. Ninety-five percent confidence intervals for each parameter were estimated as the values at 2.5 and 97.5 percentile points of the bootstrap distribution for that parameter.

SPAWNING DISTRIBUTION

Radiotelemetry techniques were used to estimate the spawning distribution of chum and coho salmon.

Radiotag Application

During the abundance experiment marking event, fish wheels were checked at least once an hour during sampling shifts. Only uninjured chum and coho salmon greater than or equal to 400 mm METF length were radiotagged, but the total catch by species was recorded. To minimize handling effects, coho salmon receiving a radio tag were either 1) taken directly out of the fish wheel basket as they were captured or 2) taken out of the fish wheel live box if the hold time did not exceed 1 h (Yanusz et al. 1999; Carlon and Evans 2007). There was no hold time restriction for chum salmon that otherwise met the tagging criteria.

A set number of radio tags was deployed each day by fish wheel and species. Average historical run timing (1981–1984) of chum and coho salmon at the ADF&G sonar and fish wheel camp at RM 6.2 of the Yentna River was used to determine the number of tags to be distributed each day over the season. Within a particular day, an equal number of radio tags was deployed among all 4 fish wheels.

All radiotagged fish were measured for METF length, a dart tag was applied adjacent to the dorsal fin, and a tissue sample (left axillary process) was collected, preserved in ethanol, and stored at the ADF&G Gene Conservation Lab in Anchorage, Alaska for later genetic assay. To minimize capture and handling-induced stress during tagging, no anesthesia was used, fish were held in water-filled tubs, and fish were restrained in padded cradles. Handling time of radiotagged fish averaged less than 1.5 minutes.

The radio transmitters used in this project were manufactured by Advanced Telemetry Systems, Inc. (ATS, Isanti, Minnesota) and operated on 18 frequencies within the 150.000 to 151.999 MHz range. Each frequency had up to 100 different transmitting patterns (i.e., pulse codes), resulting in 800 uniquely identifiable transmitters. Transmitters were cylindrical, 50 mm long × 17 mm in diameter, equipped with a 30 cm antenna, and weighed 14 g in air. The battery capacity rating of the transmitters was 126 d. Each transmitter was equipped with an activity monitor as a mortality indicator. The activity monitor changed the signal pattern to an inactive mode if the transmitter was inactive for 24 h. Radio tags were inserted through the esophagus and into the upper stomach of the fish using a 10 mm (outside diameter), 30 cm long plastic tube.

Radiotag Relocation

Tracking Stations

The migration of radiotagged chum and coho salmon upriver was tracked at 9 stations placed on major tributaries throughout the Susitna River drainage (Figure 1, Table 1). The Susitna Station tracking station was placed 3.1 RM above the Flathorn tagging site. If a radiotagged fish migrated above this "gateway" station, it officially entered the experiment.

Table 1.–Locations of tracking stations used to monitor the movements of radiotagged chum and coho salmon in the Susitna and Yentna river drainages, 2012.

		Distance (RM) from	
Drainage	Tracking station	Saltwater	Previous station
Susitna River	Susitna Station	24.9	–
	Deshka	39.6	13.5
	Sunshine	79.7	38.3
	Talkeetna	97.3	17.6
	Chulitna	106.1	26.3
	Lane Creek	113.0	33.3
Yentna River	Lower Yentna River	36.1	11.4
	Skwentna River	86.1	49.9
	Upper Yentna River	91.2	54.9

Tracking station equipment consisted of an ATS Model 4500C receiver and data logger and a self-contained power system. The equipment was housed in a waterproof enclosure and attached to the base of a 9 m mast that supported 2 Yagi antennas. An ATS Model 200 antenna switch was coupled with the 2 Yagi antennas at each tracking station. One antenna was oriented downstream and the other upstream. Signal strength and time of detection were recorded separately for each antenna and provided information on direction of travel. "Reference" radio tags were continuously detected at each station to ensure proper station operation. Information was recorded at 10-minute intervals.

The ATS receiver detected radiotagged fish and recorded signal strength, activity pattern of the transmitter (active or inactive), date, time, and location of each fish in relation to the station (i.e., upriver or downriver from the site). Radiotagged fish were considered to have passed a tracking station when the recorded signal strength indicated the transition from the downriver antenna to the upriver antenna.

Most tracking stations were visited every 7–21 days to check on the condition of the equipment and to download the radio receivers. Stations in the lower drainage (Susitna Station and Lower Yentna) were at risk of overwriting due to the large number of passing radio tags. The most remote tracking stations, Upper Yentna, Skwentna, and Chulitna, were visited every 26–41 days. Data files were downloaded using a Windows-based program on a field laptop. Data files were then saved to the ADF&G Palmer local area network.

Aerial Surveys

A fixed-wing aircraft was used to conduct aerial surveys of the entire Susitna River drainage below Devil's Canyon (Figure 1). The aircraft was equipped with an ATS Model 4520C receiver and data logger and two 4-element Yagi receiving antennas, 1 mounted on each side of the aircraft and oriented forward. Receivers contained an integrated global positioning system to identify and record latitude and longitude. Automatically recorded data included date and time of decoding, frequency and pulse code, latitude and longitude, signal strength, and activity mode of each decoded transmitter.

Estimation of Spawning Distribution

The diagnostic procedures for estimating abundance (Appendix A2) indicated that probability of capture was not uniform over time or between marking sites (fish wheels) for both chum and coho salmon. To minimize bias, spawning distribution was first estimated within each of the 4 first-event strata (described above) determined for each species. Results from the strata for each species were then combined to provide estimates of spawning distribution.

For each first-event stratum, radiotagging data were used to estimate spawning distribution as follows:

$$\hat{p}_{l,s} = \frac{n_{l,s}}{n_s} \qquad (8)$$

where $\hat{p}_{l,s}$ is the estimated proportion of salmon from stratum *s* spawning in location *l*, n_s is the number of fish radiotagged in stratum *s* that travelled to a spawning location, and $n_{l,s}$ is the number of fish from n_s that travelled to location *l*.

The total number of salmon spawning in location *l* was estimated as follows:

$$\hat{N}_l = \sum_{s=1}^{S} \hat{N}_s \hat{p}_{l,s} \qquad (9)$$

where $\hat{N}_s$ is the number of fish passing and remaining above the Flathorn Site estimated in first event stratum *s* from the Darroch (1961) model described above. The proportion of salmon spawning in each location was estimated as follows:

$$\hat{p}_l = \frac{\hat{N}_l}{\sum_{s=1}^{S} \hat{N}_s}. \tag{10}$$

Variances and 95% confidence intervals for spawning distribution estimates were estimated using bootstrap methods (Efron and Tibshirani 1993). For each bootstrap realization, bootstrap variability in the process described in Equations 8 and 9 was modeled as multinomial processes with parameters (n_s, $\hat{p}_{1,s}$,… $\hat{p}_{l,s}$).

For each bootstrap realization, the analytical *s* × *t* Darroch (1961) model was then used to generate an estimate of abundance for that bootstrap realization. One million bootstrap realizations were generated for each experiment. The standard error for each parameter estimate was calculated as the standard deviation of the bootstrap distribution for that parameter. Ninety-five percent confidence intervals for each parameter were estimated as the values at 2.5 and 97.5 percentile points of the bootstrap distribution for that parameter. Bootstrap modeling exercises to estimate uncertainty (variances) for abundance and spawning distribution were conducted concurrently for each species.

RESULTS

ABUNDANCE

Chum Salmon

During the first event in the mark–recapture experiment, a total of 2,789 chum salmon were captured in 4 fish wheels at the Flathorn Site from 9 July to 26 August 2012. Radio tags, which were used to estimate losses of marked fish from the experiment, were deployed on 400 chum salmon distributed across the run. During second event sampling, 2,923 chum salmon were inspected for marks at fish wheels at the Yentna Site (RM 6.2 of the Yentna River) and at the Mainstem Site (RM 30 of the Susitna River) (Table 2). Of these, 31 were recaptured marked fish and 2,892 were unmarked (Table 2). Data recording errors and data loss during the second event sampling resulted in incomplete information for 2 recaptured marked fish.

The tests for size-biased sampling (Appendix A1) showed no significant evidence that size selectivity occurred during either the second event sampling (P = 0.768; Figure 3) or the first sampling event (P = 0.644; Figure 4). Stratification by size was not necessary prior to estimating abundance for chum salmon.

Table 2.–Capture-recapture matrix used for Darroch (1961) model used to estimate abundance of chum salmon spawning upstream from the Flathorn Site in the Susitna River, 2012.

		Recaptures at second event strata						
First event stratum	Est. valid marks	Days 189–208	Days 209–211	Days 212–216	Days 217–220	Days 221–243	Total	Not re-captured
Days 189–207	1,119	7	0	1	0	0	8	1,111
Days 208–210	336	0	5	0	0	0	5	331
Days 211–215	348	0	0	4	3	0	7	341
Days 116–219	317	0	0	0	6	0	6	311
Days 220–239	284	0	0	0	0	5	5	279
Est. total valid marks	2,404	7	5	5	9	5	31	2,373
Est. unmarked		1,703	212	304	288	385	2,892	
Est. inspected for marks		1,710	217	309	297	390	2,923	

Note: Abundance of spawning chum salmon in the Susitna River in 2012 was estimated as 329,345 (SE 237,012).

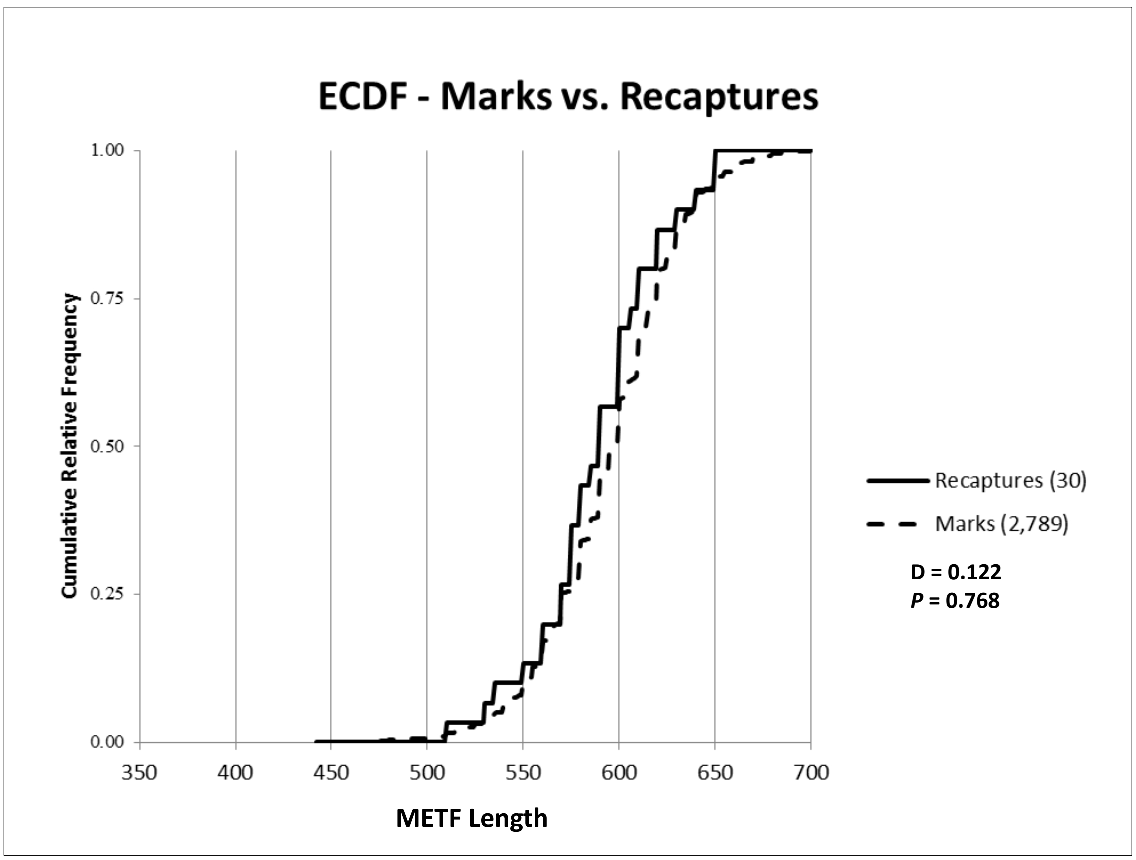

Figure 3.–Empirical cumulative distribution functions (ECDF) of length of all chum salmon marked during first-event sampling at the Flathorn Site and all recaptures during second-event sampling.

Note: The Kolmogorov-Smirnov test results for equal probability of capture based on METF length during second-event sampling were D = 0.122, *P* = 0.768. The length of 1 of the 31 recaptured fish was not obtained therefore the sample size of lengths used in the test was 30.

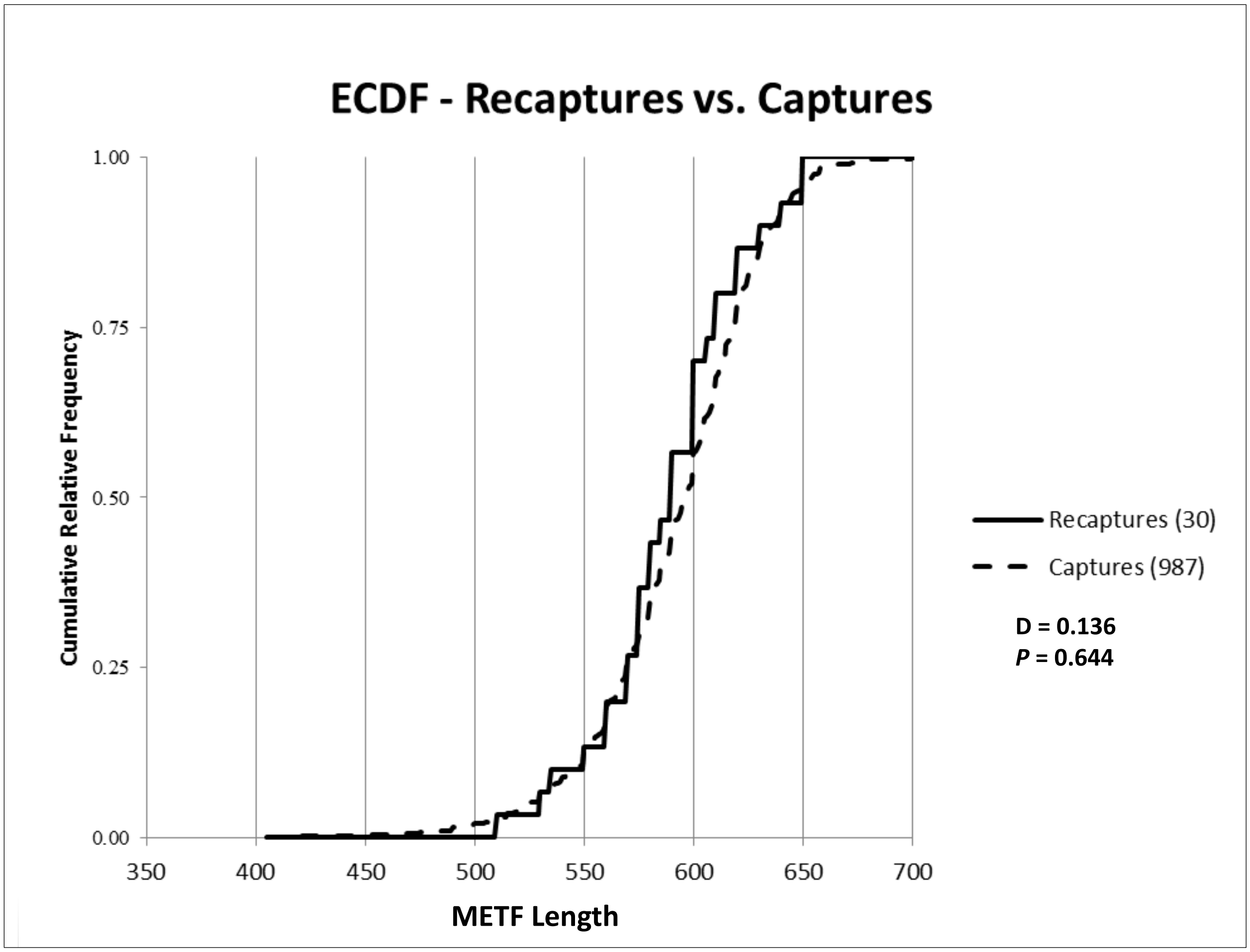

Figure 4.–Empirical cumulative distribution functions (ECDF) of length of all chum salmon inspected for marks during second-event sampling and all recaptured chum salmon during second-event sampling at mainstem Susitna River fish wheels.

Note: The Kolmogorov-Smirnov test results for equal probability of capture based on METF length during first-event sampling were D = 0.136, *P* = 0.644. The length of 1 of the 31 recaptured fish was not obtained therefore the sample size of lengths used in the test was 30.

Temporal variation in probability of capture (Appendix A2) was not detected during the second event (*P* = 0.235; Table 3) but occurred during the first sampling event (*P* < 0.001; Table 4). Geographic variation in probability of capture was detected during both the second sampling event (*P* = 0.037) and the first sampling event (*P* = 0.062). Attempts to model geographic as well as temporal variability in probability of capture did not result in admissible estimates. The partially stratified model described by Darroch (1961) incorporating only temporal variation in probability of capture was used for estimating abundance (Table 2).

During inspection of 1,710 chum salmon during second event sampling at the mainstem Susitna River fish wheels, all fish found with a missing adipose fin had retained a yellow dart tag. Therefore, tag loss was estimated to be 0.0%.

Table 3.–Results used in test for equal probability of capture (H_o) during the second-event sampling for Susitna River chum salmon, 2012.

	Period when marked				
	Days 189–207	Days 208–210	Days 211–215	Days 116–219	Days 220–239
Marks[a]	1,309	375	378	364	363
Recaptured	8	4	7	5	5
Not recaptured	1,301	371	371	359	358

Note: Results of test for temporal variation were $\chi 2 = 5.559$, $P = 0.235$; H_o was accepted.

[a] Total marks deployed; not corrected for marks lost from the experiment.

Table 4.–Results used for test for equal probability of capture (H_o) during the first-event sampling for Susitna River chum salmon, 2012.

	Period when inspected				
	Days 189–208	Days 209–211	Days 212–216	Days 217–220	Days 221–243
Inspected	1,710	217	309	297	390
Marked	7	5	5	9	5
Unmarked	1,703	212	304	288	385

Note: Results of test for temporal variation were $\chi 2 = 22.189$, $P < 0.001$; H_o was rejected.

Based on the model of Darroch (1961) (Table 2), the estimated number of chum salmon spawning upstream of the Flathorn Site in the Susitna River drainage in 2012 was 329,345 (SE 237,012) with a 95% confidence interval of 237,012 to 735,368 fish.

Coho Salmon

During the first event of the mark–recapture experiment, a total of 5,178 coho salmon were captured and tagged at the Flathorn Site from 8 July to 26 August 2012. Radio tags were deployed on 399 coho salmon distributed across the run. These radiotagged fish were used to estimate losses of marked fish from the experiment. During second-event sampling, 5,444 coho salmon were inspected for marks at fish wheels at the Yentna Site and at the Mainstem Site (Table 5). Of these, 190 were recaptured marked fish and 5,254 were unmarked (Table 5). Data recording errors and data loss during the second-event sampling resulted in incomplete information for 5 recaptured marked fish.

The tests for size-biased sampling (Appendix A1) showed no significant evidence that size selectivity occurred during either the second-event sampling ($P = 0.798$, Figure 5) or the first sampling event ($P = 0.604$, Figure 6). Stratification by size was not necessary prior to estimating abundance for coho salmon.

Table 5.–Capture-recapture matrix used for Darroch (1961) model used to estimate abundance of coho salmon spawning upstream from the Flathorn Site in the Susitna River, 2012.

		Recaptures at second event strata							
		Yentna Site event days			Mainstem Site event days				
First event stratum	Est. valid marks	189–216	217–219	220–243	189–216	217–219	220–243	Total	Not recaptured
FW 1									
Days 189–212	2,119	77	7	1	4	1	0	90	2,029
Days 213–216	377	3	12	8	1	0	0	25	352
Days 217–239	735	0	2	34	0	0	6	42	692
FW 2–4									
Days 189–214	966	4	0	0	6	0	1	11	955
Days 215–217	153	0	5	4	0	3	0	12	140
Days 218–239	253	0	0	3	0	0	6	9	244
Est. total valid marks	4,602	84	27	51	11	4	13	190	4,412
Est. unmarked		3,069	545	619	697	105	219	5,254	
Est. inspected for marks		3,153	572	670	708	109	232	5,444	

Note: FW means fish wheel. Estimated abundance of spawning chum salmon in the Susitna River is 184,316 (SE 34,910).

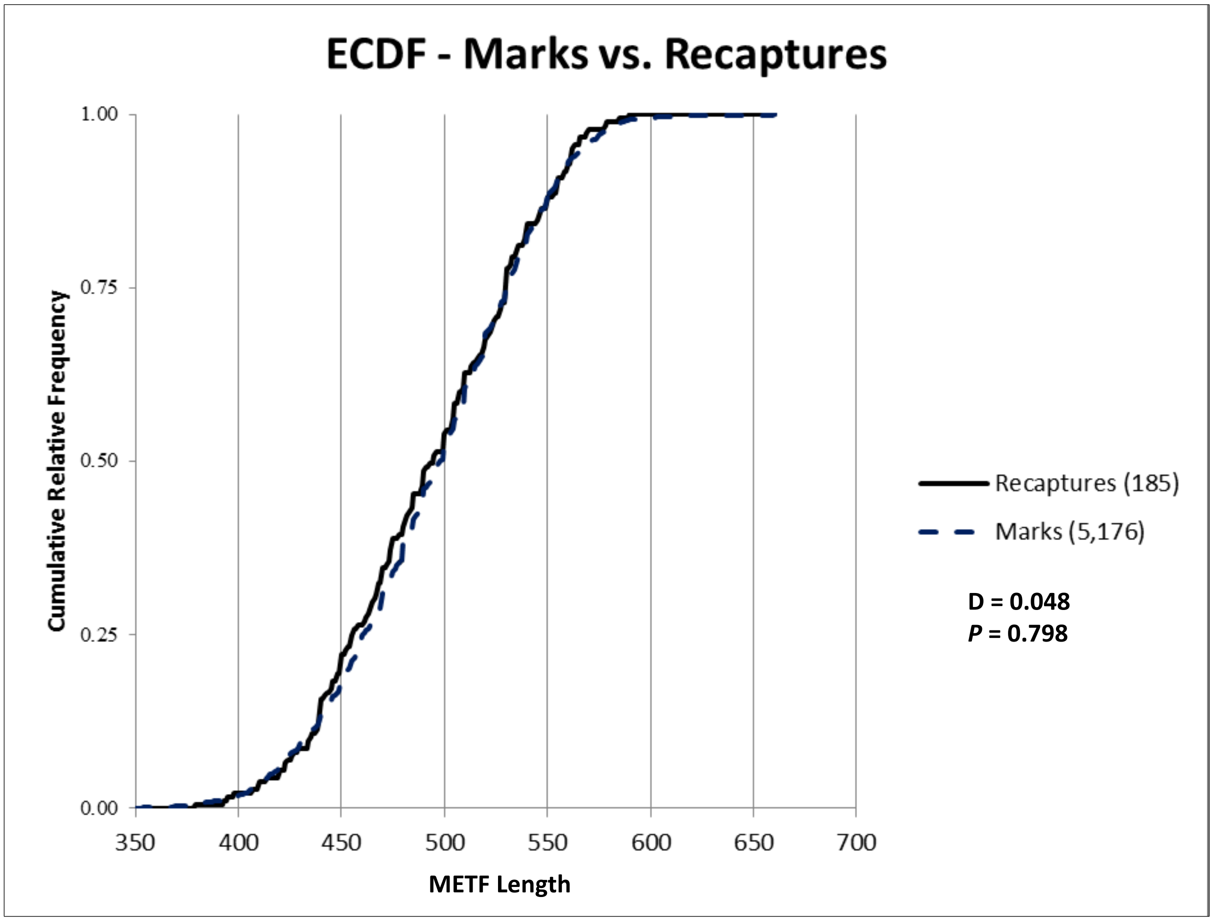

Figure 5.–Empirical cumulative distribution functions (ECDF) of length of all coho salmon marked during first-event sampling at the Flathorn Site and all recaptures during second-event sampling.

Note: The Kolmogorov-Smirnov test results for equal probability of capture based on METF length during second-event sampling were D = 0.048, *P* = 0.798. The lengths of 5 of the 190 recaptured fish were not obtained, and therefore the sample size of lengths used in the test was 185. The lengths of 2 of the 5,178 fish originally marked were not collected or were recorded incorrectly.

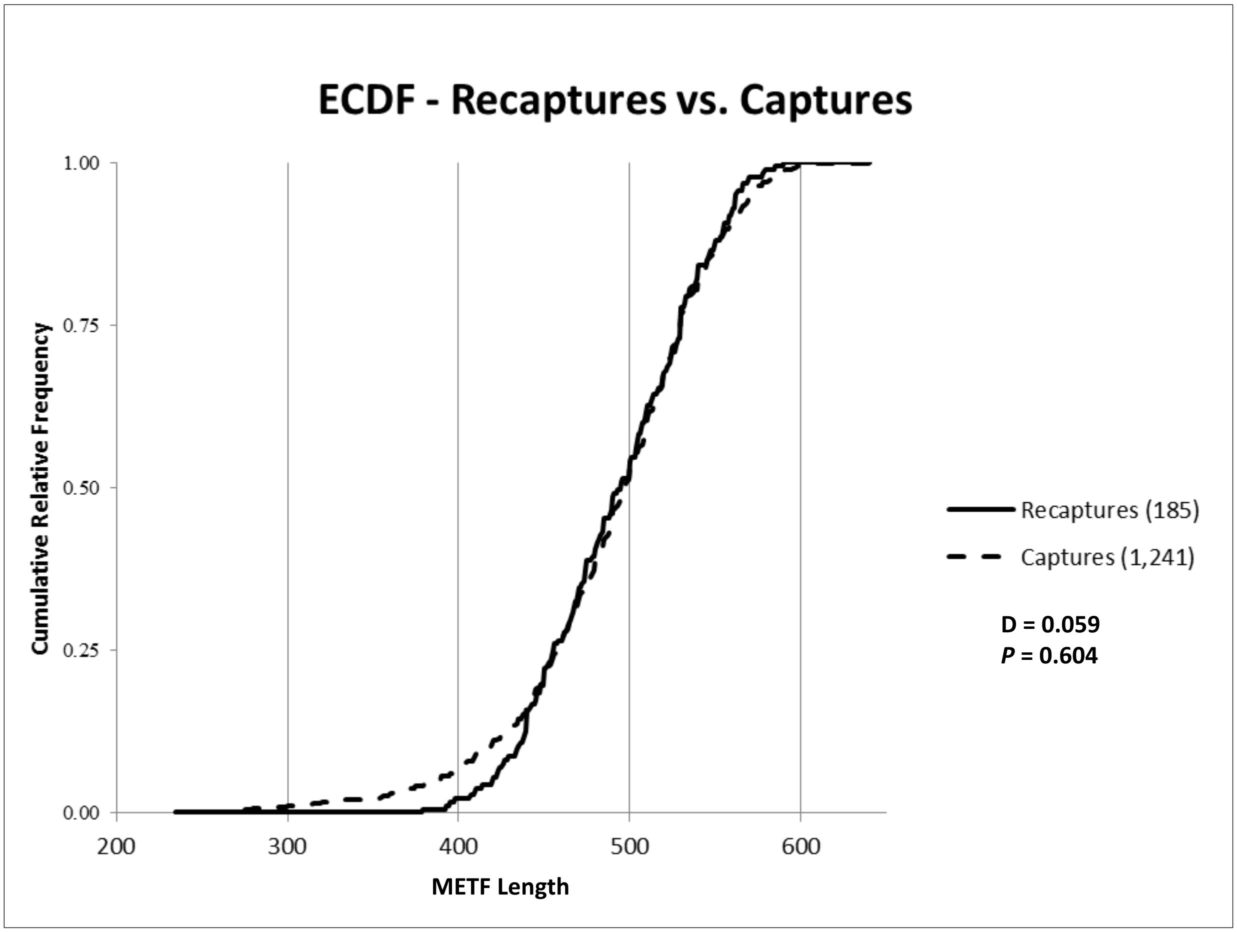

Figure 6.–Empirical cumulative distribution functions (ECDF) of length of a sample of coho salmon inspected for marks during second event sampling and all recaptured coho salmon during second-event sampling at the Mainstem Site and the Yentna Site fish wheels.

Note: The Kolmogorov-Smirnov test results for equal probability of capture based on METF length during first-event sampling were D = 0.059, *P* = 0.604. The lengths of 5 of the 190 recaptured fish were not obtained therefore the sample size of lengths used in the test was 185.

Temporal and geographic variation in probability of capture (Appendix A2) was detected during both second ($P < 0.001$) and first ($P < 0.001$) sampling events (Tables 6 and 7). As a result, the partially stratified model described by Darroch (1961) was necessary for estimating abundance (Table 5).

Table 6.–Results used to test for equal probability of capture (H_o) during the second-event sampling for Susitna River coho salmon, 2012.

	Area and time where marked					
	Fish wheel 1 event days			Fish wheels 2–4 event days		
	189–212	213–216	217–239	189–214	215–217	218–239
Marks [a]	2,406	411	812	1,079	165	305
Recaptured	88	24	41	11	12	9
Not recaptured	2,318	387	771	1,068	153	296

Note: Results of test for temporal (event days) and geographical variation were $\chi 2 = 33.635$, $P < 0.001$; H_o was rejected.

[a] Total marks deployed; not corrected for marks lost from the experiment.

Table 7.–Test for temporal and geographical variation of capture for Susitna River coho salmon during first-event sampling, 2012.

	Area and time where inspected					
	Yentna Site event days			Mainstem Site event days		
	189–216	217–219	220–243	189–216	217–219	220–243
Inspected	3,153	572	670	708	109	232
Marked	84	27	51	11	4	13
Unmarked	3,069	545	619	697	105	219

Note: Results of test for temporal (event days) and geographical (recapture site) variation were $\chi^2 = 53.720$, $P < 0.001$; H_o was rejected.

During inspection of 1,049 coho salmon during second-event sampling at the mainstem Susitna River fish wheels, all fish found with missing adipose fins had retained a yellow dart tag. Tag loss was estimated to be 0.0%.

Based on the model of Darroch (1961) (Table 5), the estimated number of coho salmon spawning upstream of the Flathorn site in the Susitna River drainage in 2012 was 184,316 (SE 34,910) with a 95% confidence interval of 139,469 to 267,485 fish.

SPAWNING DISTRIBUTION

Radiotag Application

In 2012, a total of 2,789 chum salmon captured at fish wheels (FW) operated at the Flathorn Site from 9 July to 26 August were tagged with dart tags; 400 of these were also radiotagged. A total of 101 radiotagged chum salmon were released from FW 1, 102 from FW 2, 94 from FW 3, and 103 from FW 4. A total of 5,178 coho salmon captured among the 4 fish wheels; 399 of these were also radiotagged. A total of 100 radiotagged coho salmon were released from FW 1, 99 from FW 2, 101 from FW 3, and 99 from FW 4. Ninety percent of chum salmon and 96% of coho salmon radio tags were deployed between 12 July and 13 August (Table 8).

Table 8.–Chum and coho salmon radio tags deployed by week at the Flathorn Site on the Susitna River, 2012.

Dates	Chum salmon	Coho salmon
8–14 Jul	33	18
15–21 Jul	80	102
22–28 Jul	98	108
29 Jul–4 Aug	88	88
5–11 Aug	48	63
12–18 Aug	28	18
19 –25 Aug	23	2
26 Aug–1 Sep	2	0
Total	400	399

Tracking Stations

In the Yentna River drainage, the lower Yentna River tracking station operated 9 May through 12 September 2012, the upper Yentna River tracking station operated 6 June through 2 October 2012, and the Skwentna River station operated 5 June through 19 September 2012.

The mainstem Susitna River tracking stations were installed between 9 May and 26 May. The Deshka River tracking station operated 15 May through 12 September except during 12 through 17 July. Data from the Deshka River tracking station were apparently overwritten, possibly due to high fish passage rates. Data were collected at the Skwentna River tracking station from 5 June through 15 August, when the power supply failed. The Talkeetna tracking station operated from 23 May until flooding on 20 September ended operation. Other Susitna River mainstem tracking stations were removed for the season between 10 September and 4 October, 2012.

Aerial Surveys

Aerial surveys of the mainstem Susitna River were conducted on 29 June; 10, 17, 18, and 31 July; 6, 7, 9, 10, 22, 24, and 29 August; 7 and 26 September; and 1 October 2012. Surveys of the Yentna River drainage were completed on 8, 25, and 28 August; 11 and 27 September; and 3 October 2012. Drainagewide surveys were conducted on 3 August and 13 September. Of the 799 radiotagged salmon, 730 (91.4%) final locations were assigned based on aerial surveys and corroborated with ground tracking stations. Thirty-three of the 730 tagged fish assigned a final location were never located past the Susitna Station tracking station. Of the 69 fish not assigned a final location, 50 were never detected by either aerial or ground tracking devices, and 19 were harvested by sport anglers (Table 9).

Table 9.–Movement and migration pattern descriptions used to determine the final spawning location of radiotagged salmon relocated during aerial surveys in 2012.

		Chum salmon		Coho salmon	
Code	Movement description	Number	Percent	Number	Percent
0	Never relocated.	26	6.5	24	6.0
1	Did not migrate upstream of Susitna Station.	28	7.0	5	1.3
2	Progressive upstream movement through all aerial surveys.	68	17.0	206	51.6
3	Progressive upstream movement except the last 1–2 aerial surveys; assigned the farthest upstream location.	132	33.0	64	16.0
4	Initially displayed upstream movement but then displayed downstream movement >2 aerial surveys; assigned farthest upstream location.	76	19.0	13	3.3
5	A cluster of locations (within 20 miles); assigned a known location in the middle of cluster.	36	9.0	29	7.3
6	A cluster of locations except 1 outlier; assigned location in the middle of cluster, unless the outlier was observed during a late season (>15 Sep) survey, then it was assigned the farthest upstream location.	3	0.8	1	0.3
7	Migrated up river A and then had >2 locations up river B. If strong signal strengths (>120) exist among cluster in river B, then fish was assigned to river B, otherwise river A.	18	4.5	18	4.5
8	Single aerial relocation only.	10	2.5	24	6.0
9	Caught by sport angler.	3	0.8	15	3.8
10	Aerial records exist, but station is farthest upstream location.	0	0.0	0	0.0
11	No aerial records; farthest upstream station used.	0	0.0	0	0.0
	Total	400	100.0	399	100.0

Spawning Locations

Radiotagged salmon were assigned 1 of 11 movement and migration pattern descriptions. Of the 730 radiotagged salmon relocated by aerial surveys, only 17.0% of chum salmon but 51.6% of coho salmon displayed progressive and constant upstream movement to their assumed spawning location (Table 9). An additional 33.0% of chum salmon and 16.0% of coho salmon displayed progressive and constant upstream movement except in the last 1 to 2 surveys.

The Susitna Station gateway tracking station was approximately 1.8 miles upstream from the nearest fish wheel and regarded as the point at which radiotagged salmon entered the mark–recapture experiments. Aerial survey and tracking station data were used to assign a putative final spawning location to each chum and coho salmon that migrated upstream of the Susitna Station tracking station (Tables 10–12). Of the 400 radiotagged chum salmon, 343 (85.8%) were assigned a putative spawning location upstream of Susitna Station and were included in the analyses (Tables 10 and 12, Figures 7–11). Of the 399 radiotagged coho salmon, 355 (89.0%) were assigned a putative spawning location upstream of Susitna Station and were included in the analyses (Tables 11 and 12, Figures 12–16).

Of the radiotagged fish, 27 chum and 5 coho salmon did not migrate upstream of the Susitna Station (Table 12) and were not assigned a putative final spawning location. These include 1 chum salmon that was located in Alexander Creek, 8.7 RM downstream of the Flathorn tagging site. Twenty-six radiotagged chum and 24 radiotagged coho salmon were not documented by stationary towers or aerial surveys (Table 9). Fish that were not detected, fish that did not migrate past the Susitna Station, and harvested fish were excluded from the mark–recapture experiment and locations were not reflected in the final distribution map for each species.

The final putative spawning locations indicate that chum and coho salmon were strongly bank oriented at the Flathorn tagging site. Of the 87 chum salmon tagged on FW 1 that migrated upstream of the gateway station, 74 (85.1%) migrated up the Yentna River (Figure 8). Of the 92 chum salmon tagged on FW 4 that migrated upstream of the gateway station, 89 (96.7%) migrated up the mainstem Susitna River (Figure 11). Of the 89 coho salmon tagged on FW 1 that migrated upstream of the gateway station, 85 (95.5%) migrated up Yentna River (Figure 13). Of the 90 coho salmon tagged on FW 4 that migrated upstream of the gateway station, 89 (98.9%) migrated up the mainstem Susitna River (Figure 16).

Sport anglers voluntarily returned radio tag information from 2 sport caught chum salmon: 1 from Willow Creek and 1 from Montana Creek. A third chum salmon was harvested from Willow Creek but angler information was not available. Sport anglers voluntarily returned information on 14 of 15 radiotagged sport caught coho salmon. Ten were taken from the Susitna River drainage: 1 from Alexander Creek; 3 from the Deshka River; 1 each from Goose, Rabideaux, and Sunshine creeks; and 3 from the Talkeetna River drainage. Three fish were taken in the Yentna River drainage: 1 downstream of Lake Creek, 1 from Lake Creek, and 1 from the Talachulitna River. There was no information for 2 sport harvested coho salmon.

Table 10.–Unweighted terminal distribution by fish wheel (number of fish and percent) of radiotagged chum salmon in the Susitna River drainage in 2012.

	Fish wheel							
	FW 1		FW 2		FW 3		FW 4	
Location	Number	Percent	Number	Percent	Number	Percent	Number	Percent
RM 0.0–24.0 Susitna River [a]	8	8.4	12	12.9	6	6.7	2	2.1
RM 24.1–98.0 Susitna River	4	4.2	21	22.6	15	16.9	25	26.6
RM 98.1–154.1 Susitna River		0.0	6	6.5	9	10.1	10	10.6
Eastside Parks Hwy [b]	2	2.1	8	8.6	6	6.7	15	16.0
Deshka River		0.0		0.0		0.0	2	2.1
Talkeetna River	5	5.3	23	24.7	15	16.9	22	23.4
Chulitna River	2	2.1	9	9.7	12	13.5	15	16.0
Tokositna River		0.0		0.0	2	2.2		0.0
Yentna River below Skwentna River confl.	9	9.5	4	4.3	3	3.4		0.0
Yentna River above Skwentna River confl.	9	9.5	7	7.5	8	9.0		0.0
Kahiltna River		0.0		0.0		0.0		0.0
Lake Creek	3	3.2		0.0	2	2.2	1	1.1
RM 0.0–16.0 Skwentna River	3	3.2		0.0		0.0		0.0
RM 16.1+ Skwentna River	31	32.6	1	1.1	5	5.6	1	1.1
Talachulitna River	11	11.6		0.0	4	4.5		0.0
Johnson Creek		0.0	2	2.2		0.0		0.0
Kichatna River	8	8.4		0.0	2	2.2	1	1.1
Total [c]	95	100.0	93	100.0	89	100.0	94	100.0

[a] Terminal locations between RM 0and RM 24 Susitna River account for all radio tags that did not migrate above the “gateway” tracking station (Susitna Station) including those assigned to Alexander Creek.

[b] Includes Willow Creek, Kashwitna River, Sheep Creek, and Montana Creek that drain into the Susitna River along the Parks Highway.

[c] The total does not include 26 chum salmon never relocated by aerial or ground relocation methods (6 from FW 1, 6 from FW 2, 5 from FW 3, and 9 from FW 4) and 3 chum salmon that were harvested by sport anglers.

Table 11.–Unweighted terminal distribution by fish wheel (number of fish and percent) of radiotagged coho salmon in the Susitna drainage in 2012.

	Fish wheel									
	FW 1		FW 2		FW 3		FW 4		Total	
Location	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent
RM 0–24 Susitna River [a]	1	1.1	3	3.4	1	1.1		0.0	5	1.4
RM 24.1–98.0 Susitna River	2	2.2	15	16.9	15	16.5	15	16.7	47	13.1
RM 98.1–154.1 Susitna River		0.0	2	2.2	4	4.4	1	1.1	7	1.9
East Side Parks Hwy [b]		0.0	5	5.6	15	16.5	16	17.8	36	10.0
Deshka River	1	1.1	5	5.6	12	13.2	7	7.8	25	6.9
Talkeetna River		0.0	9	10.1	10	11.0	12	13.3	31	8.6
Chulitna River	1	1.1	11	12.4	16	17.6	25	27.8	53	14.7
Tokositna River		0.0	12	13.5	12	13.2	13	14.4	37	10.3
Yentna River below Skwentna River confl.	24	26.7	2	2.2		0.0		0.0	26	7.2
Yentna River above Skwentna River confl.	12	13.3	3	3.4		0.0		0.0	15	4.2
Kahiltna River	10	11.1	2	2.2		0.0	1	1.1	13	3.6
Lake Creek	7	7.8	7	7.9		0.0		0.0	14	3.9
RM 0.0-16.0 Skwentna River	3	3.3	1	1.1		0.0		0.0	4	1.1
RM 16.1+ Skwentna River	10	11.1	3	3.4	1	1.1		0.0	14	3.9
Talachulitna River	14	15.6	6	6.7	1	1.1		0.0	21	5.8
Johnson Creek	1	1.1		0.0		0.0		0.0	1	0.3
Kichatna River	4	4.4	3	3.4	4	4.4		0.0	11	3.1
Total [c]	90	100.0	89	100.0	91	100.0	90	100.0	360	100.0

[a] Terminal locations between RM 0 and RM 24 Susitna River account for all radio tags that did not migrate above the "gateway" tracking station (Susitna Station) including those assigned to Alexander Creek.

[b] Includes Willow Creek, Kashwitna River, Sheep Creek, and Montana Creek that drain into the Susitna River along the Parks Highway.

[c] The total does not include 24 coho salmon never relocated by aerial or ground relocation methods (7 from FW 1, 6 from FW 2, 7 from FW 3 and 4 from FW 4).

Table 12.–Terminal distribution summary of radiotagged chum and coho salmon in the Susitna River drainage, 2012.

			Chum salmon		Coho salmon	
Drainage	Region	Nearby tributaries	Number [a]	Percent	Number [b]	Percent
Susitna River						
	Susitna River mainstem (RM 0.0–24.0) [c]		27	7.3	5	1.4
		Alexander Creek	1	0.3	0	0.0
	Susitna River mainstem (RM 24.1–98.0)		66	17.8	51	14.2
		Deshka River	2	0.5	25	6.9
		Willow Creek	11	3.0	6	1.7
		Little Willow Creek	5	1.3	10	2.8
		Kashwitna River	2	0.5	3	0.8
		Sheep Creek	3	0.8	7	1.9
		Montana Creek	9	2.4	6	1.7
	Talkeetna River		22	5.9	17	4.7
		Chunilna River (Clear Creek)	42	11.3	11	3.1
		Sheep River	0	0.0	0	0.0
		Iron Creek	0	0.0	0	0.0
		Prairie Creek–Stephan Lake	0	0.0	3	0.8
	Upper Susitna River mainstem (RM 98.0–154.0)		9	2.4	2	0.6
		Tributaries	16	4.3	5	1.4
	Chulitna River		38	10.2	52	14.4
		Byers Creek	0	0.0	1	0.3
		Tokositna River	2	0.5	37	10.3
		Swan Lake	0	0.0	0	0.0

-continued-

Drainage	Region	Nearby tributaries	Chum salmon Number [a]	Chum salmon Percent	Coho salmon Number [b]	Coho salmon Percent
Yentna River						
	Yentna River mainstem below Skwentna River		24	6.5	18	5.0
		Kahiltna River	0	0.0	13	3.6
		Peters Creek	0	0.0	8	2.2
		Lake Creek	6	1.6	14	3.9
		Chelatna Lake	0	0.0	0	0.0
	Yentna River mainstem above Skwentna River		16	4.3	15	4.2
	Lower Skwentna River mainstem (RM 0.0–16.0)		3	0.8	3	0.8
		Tributaries	0	0.0	0	0.0
		Shell Creek–Shell Lake	0	0.0	1	0.3
		Talachulitna River	5	1.3	8	2.2
		Talachulitna Creek–Judd Lake	10	2.7	13	3.6
	Upper Skwentna River mainstem (RM 16.1+)		39	10.5	12	3.3
		Hayes River	0	0.0	2	0.6
	Hewitt Creek–Hewitt Lake		0	0.0	0	0.0
	Johnson Creek		2	0.5	1	0.3
	Kichatna River		11	3.0	11	3.1
	Total		371	100.0	360	100.0

[a] Twenty-six deployed chum salmon radio tags were never detected via either aerial or ground relocation methods.

[b] Twenty-four deployed coho salmon radio tags were never detected via either aerial or ground relocation methods.

[c] Terminal locations between Susitna River mainstem RM 0 and RM 24 account for all radio tags that did not migrate above the gateway tracking station (Susitna Station). This includes 1 chum salmon that was assigned a putative spawning location of Alexander Creek, which is 8.7 mi downstream of the Flathorn tagging site.

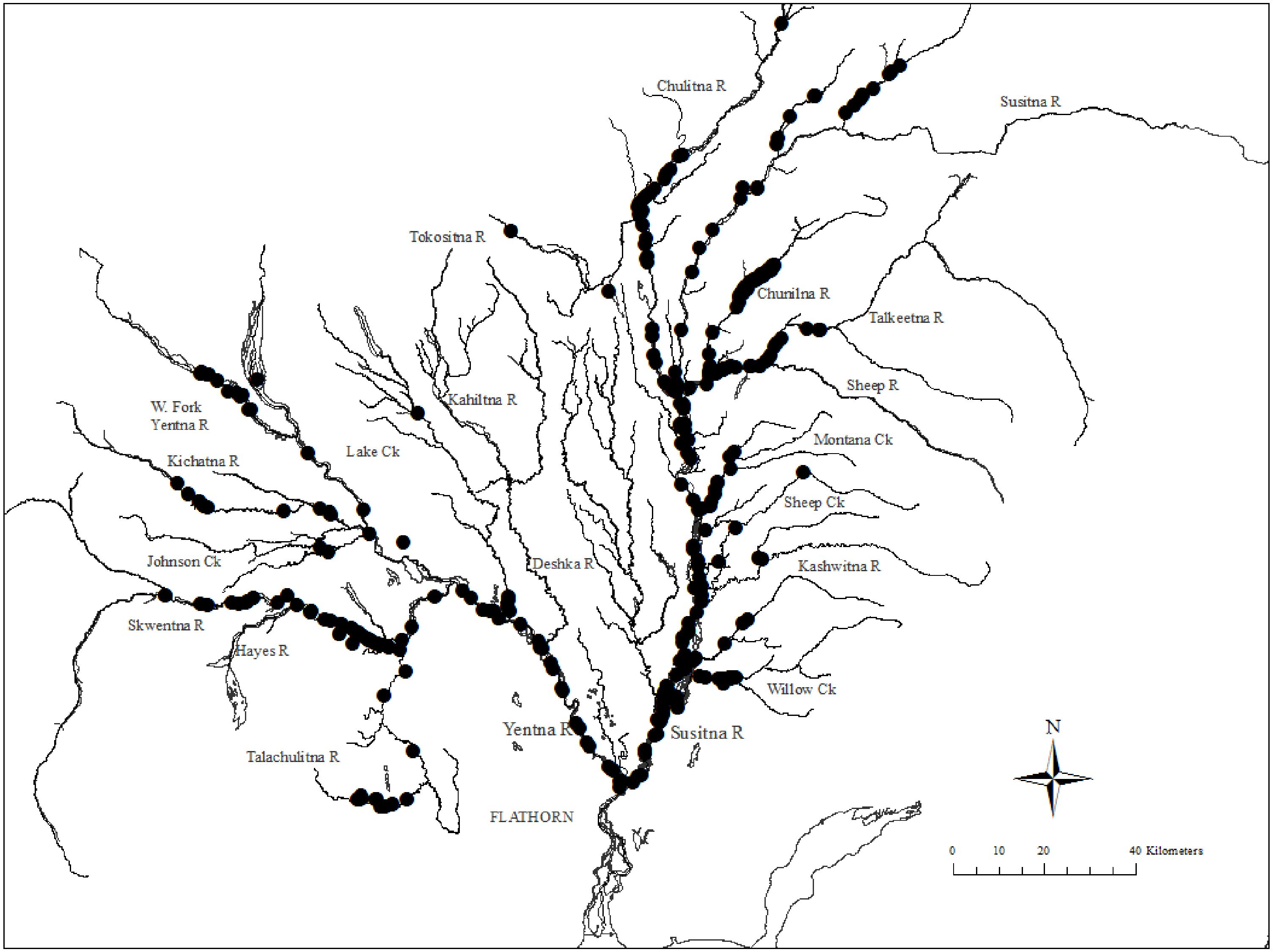

Figure 7.–Final locations of chum salmon radiotagged at all fish wheels in 2012.

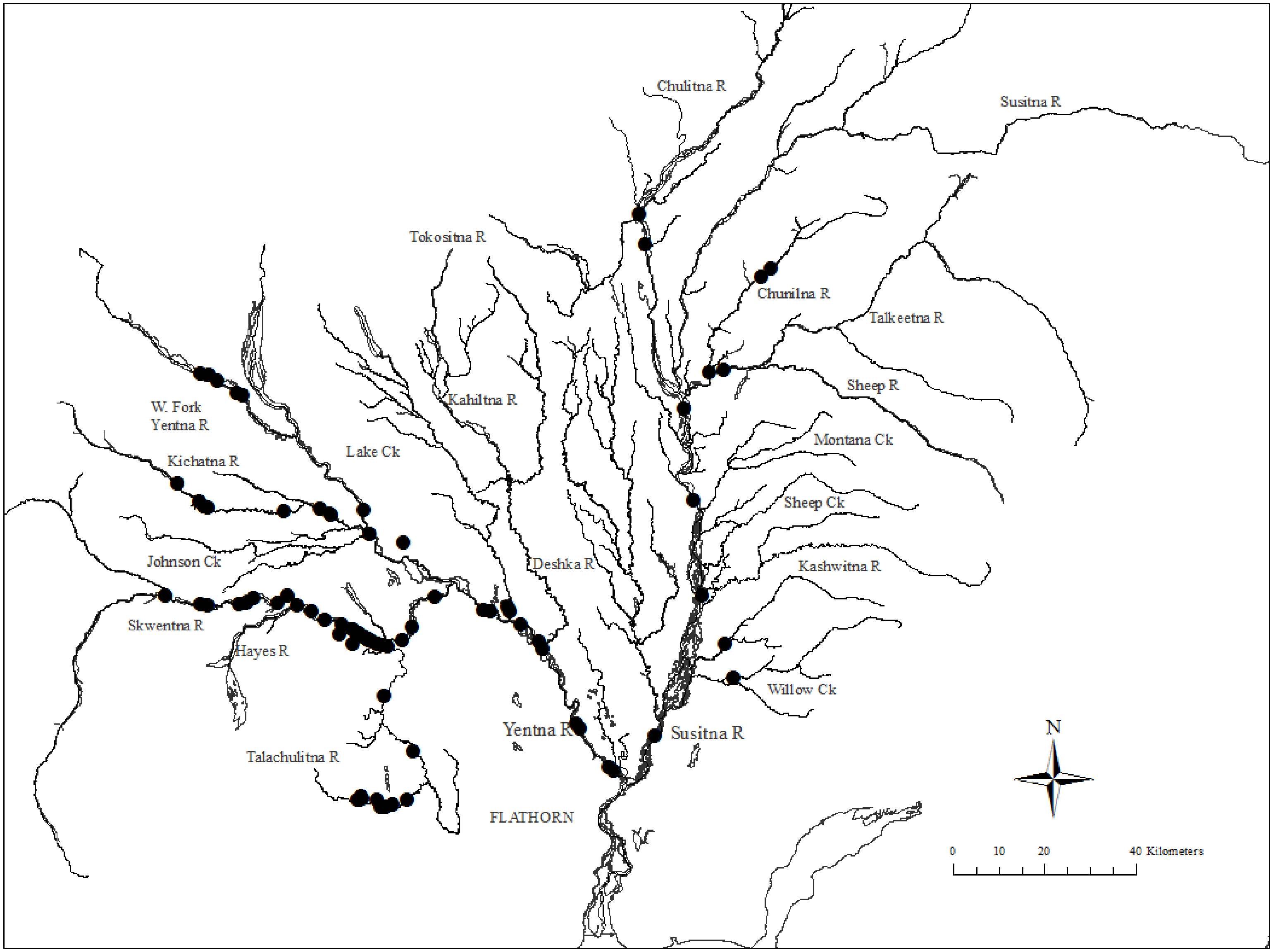

Figure 8.–Final locations of chum salmon radiotagged at FW 1, 2012.

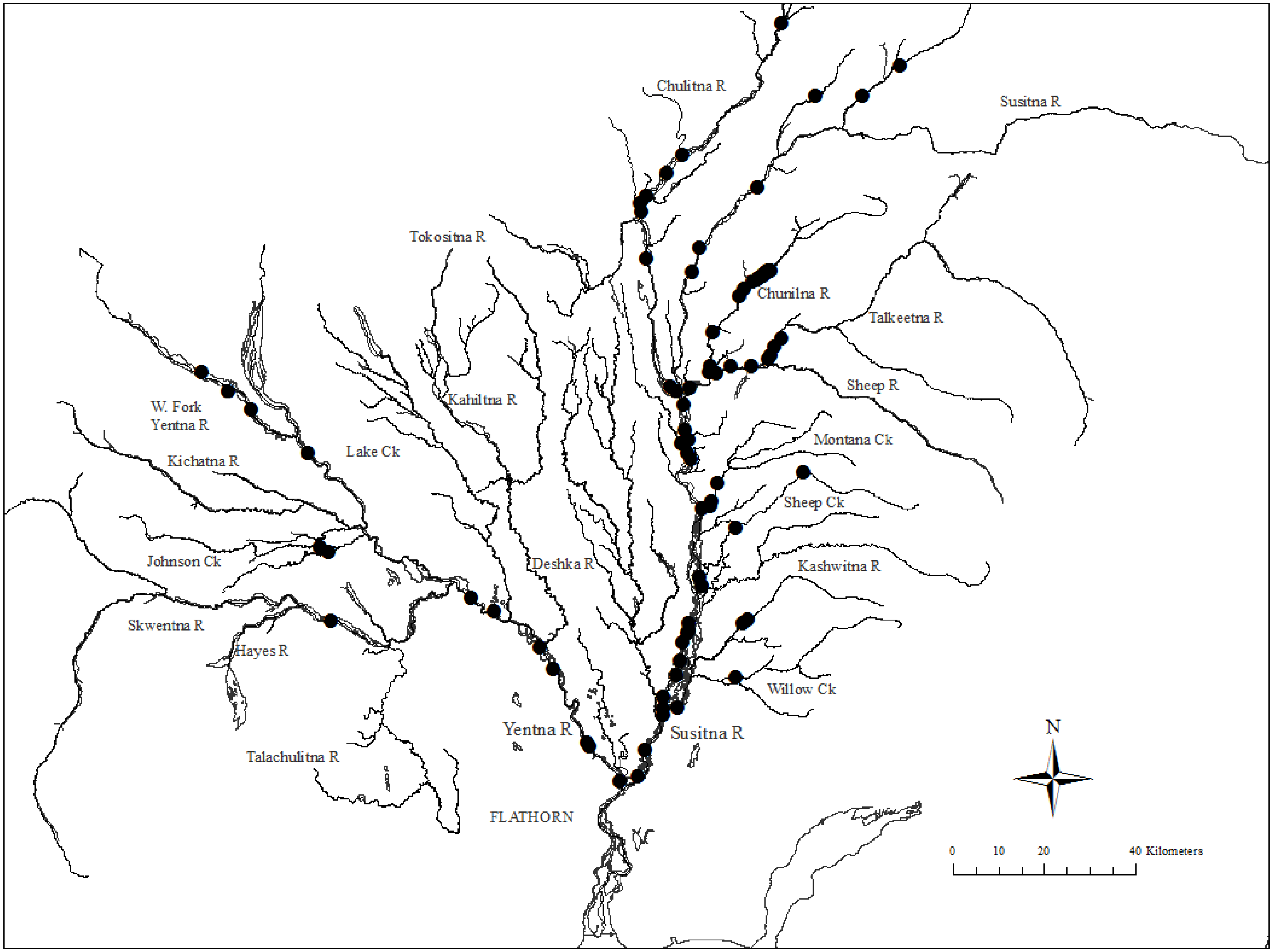

Figure 9.–Final locations of chum salmon radiotagged at FW 2, 2012.

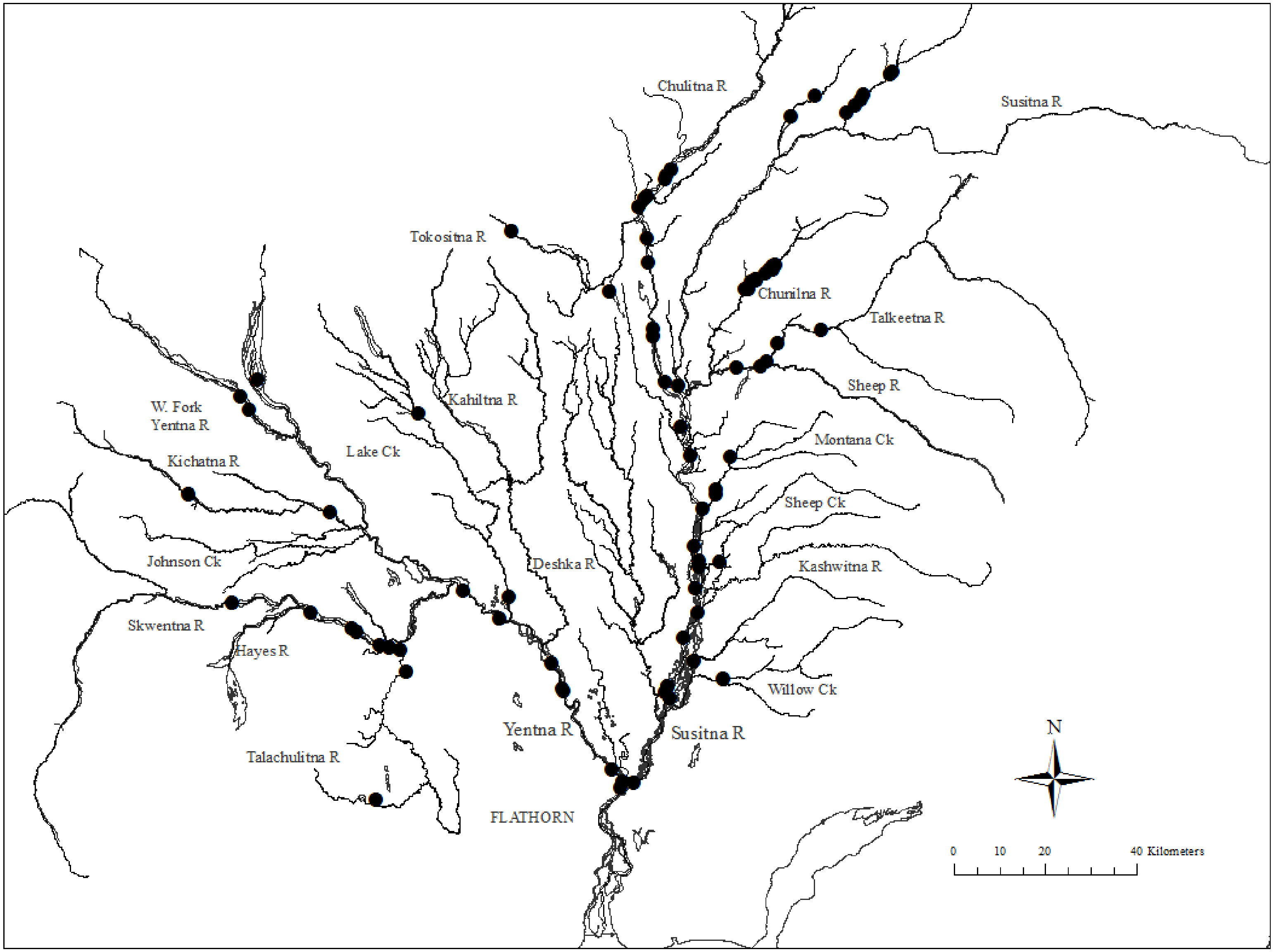

Figure 10.–Final locations of chum salmon radiotagged at FW 3, 2012.

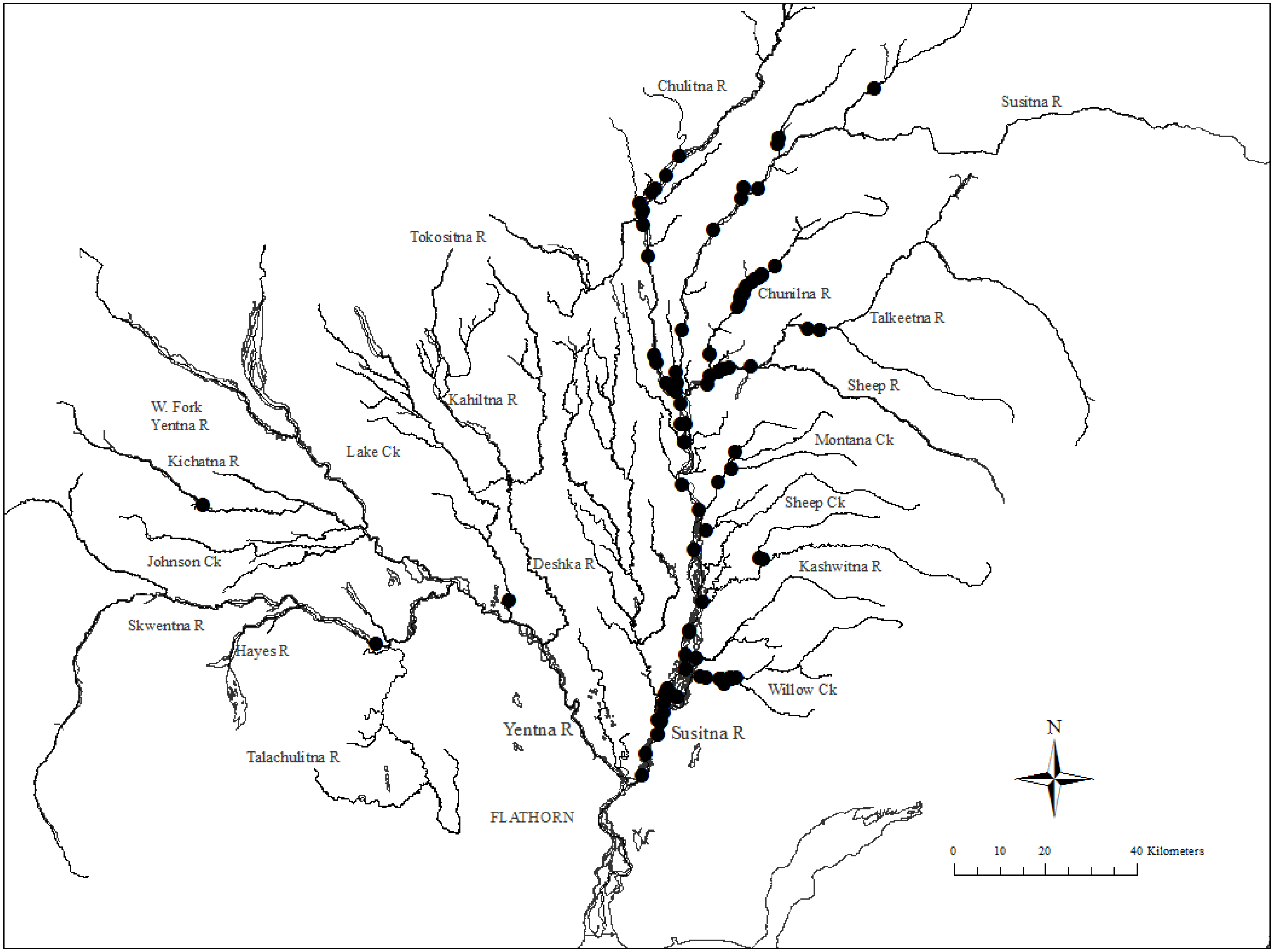

Figure 11.–Final locations of chum salmon radiotagged at FW 4, 2012.

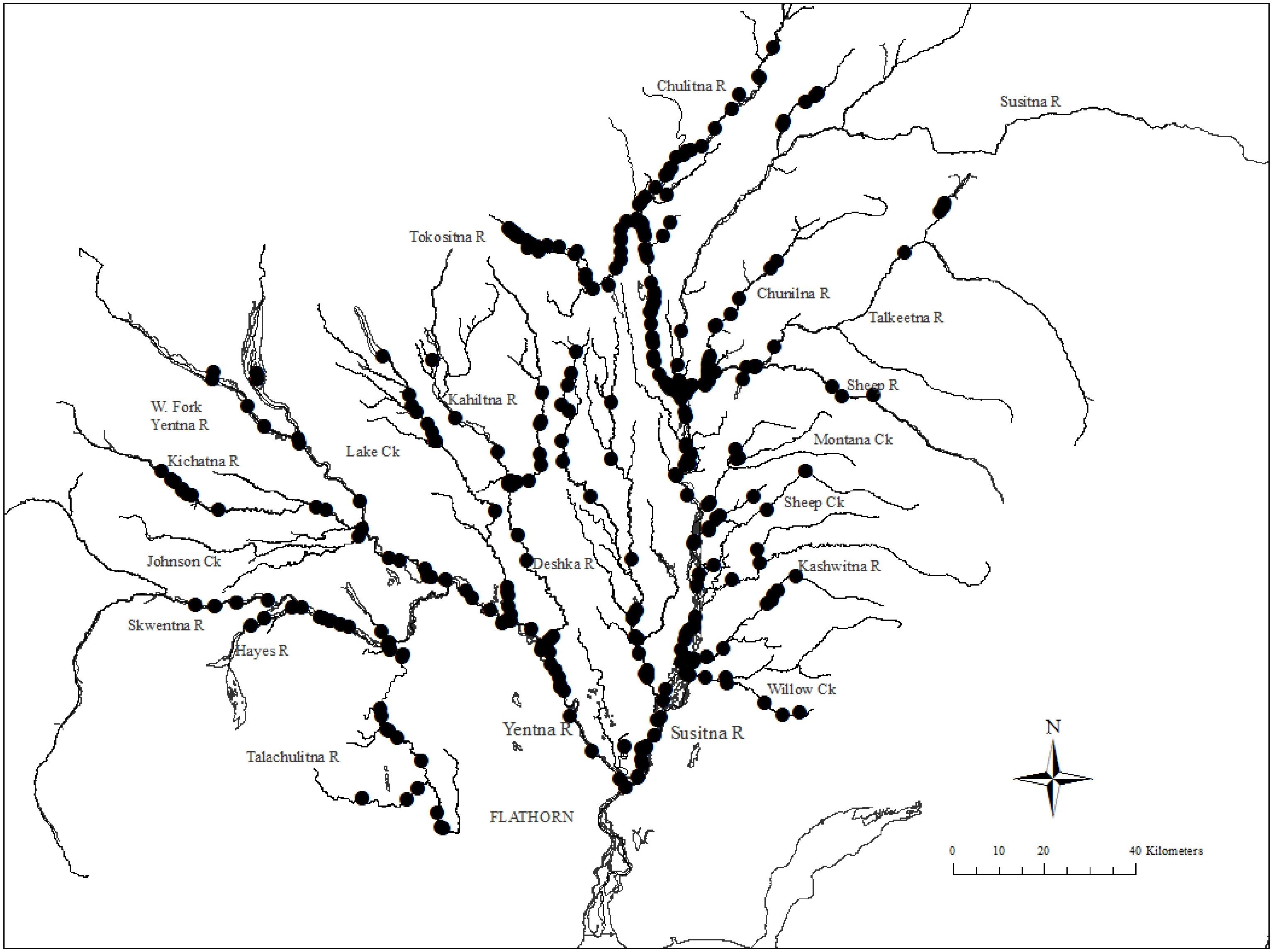

Figure 12.–Final locations of coho salmon radiotagged at all fish wheels in 2012.

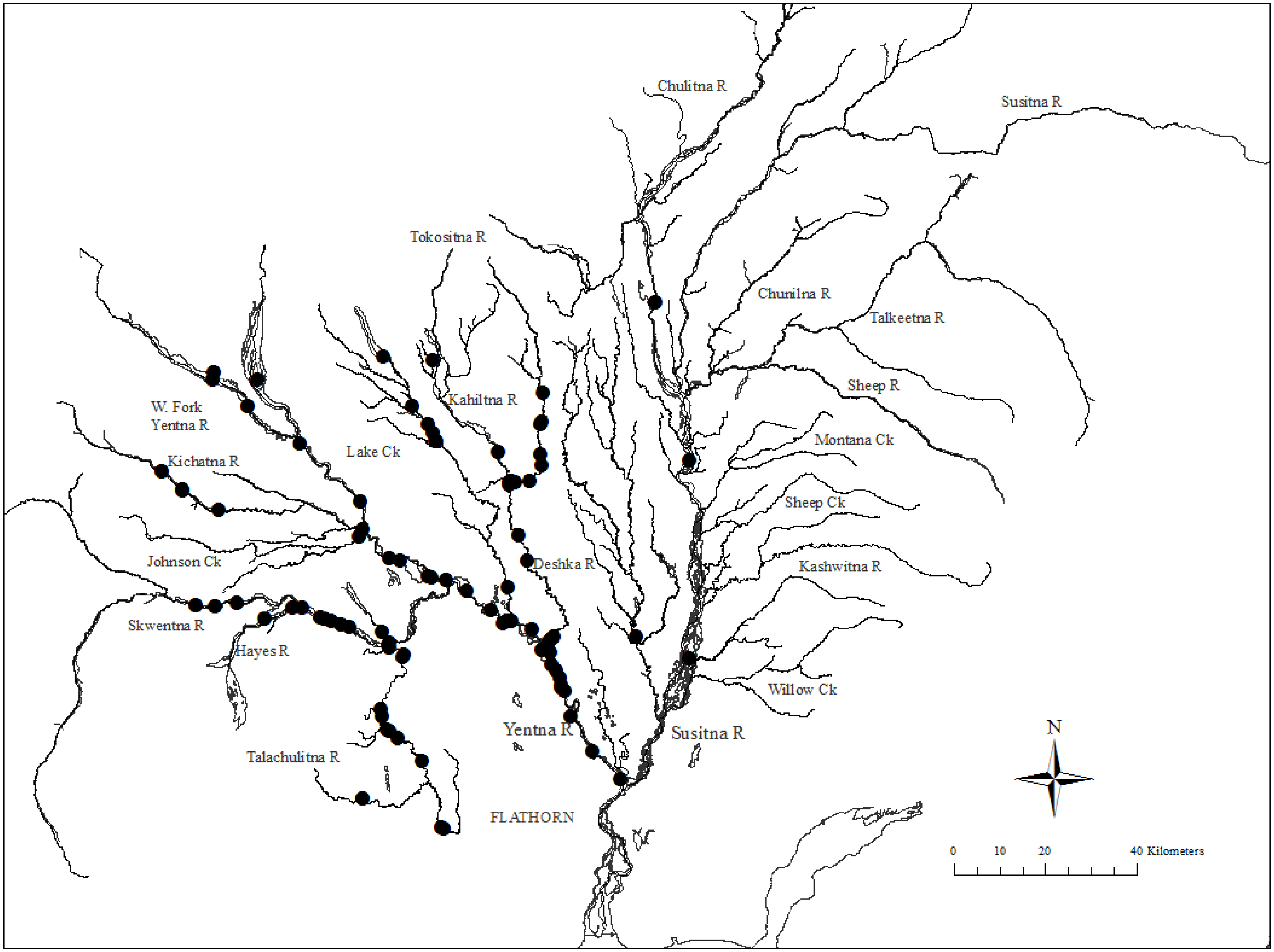

Figure 13.–Final locations of coho salmon radiotagged at FW 1, 2012.

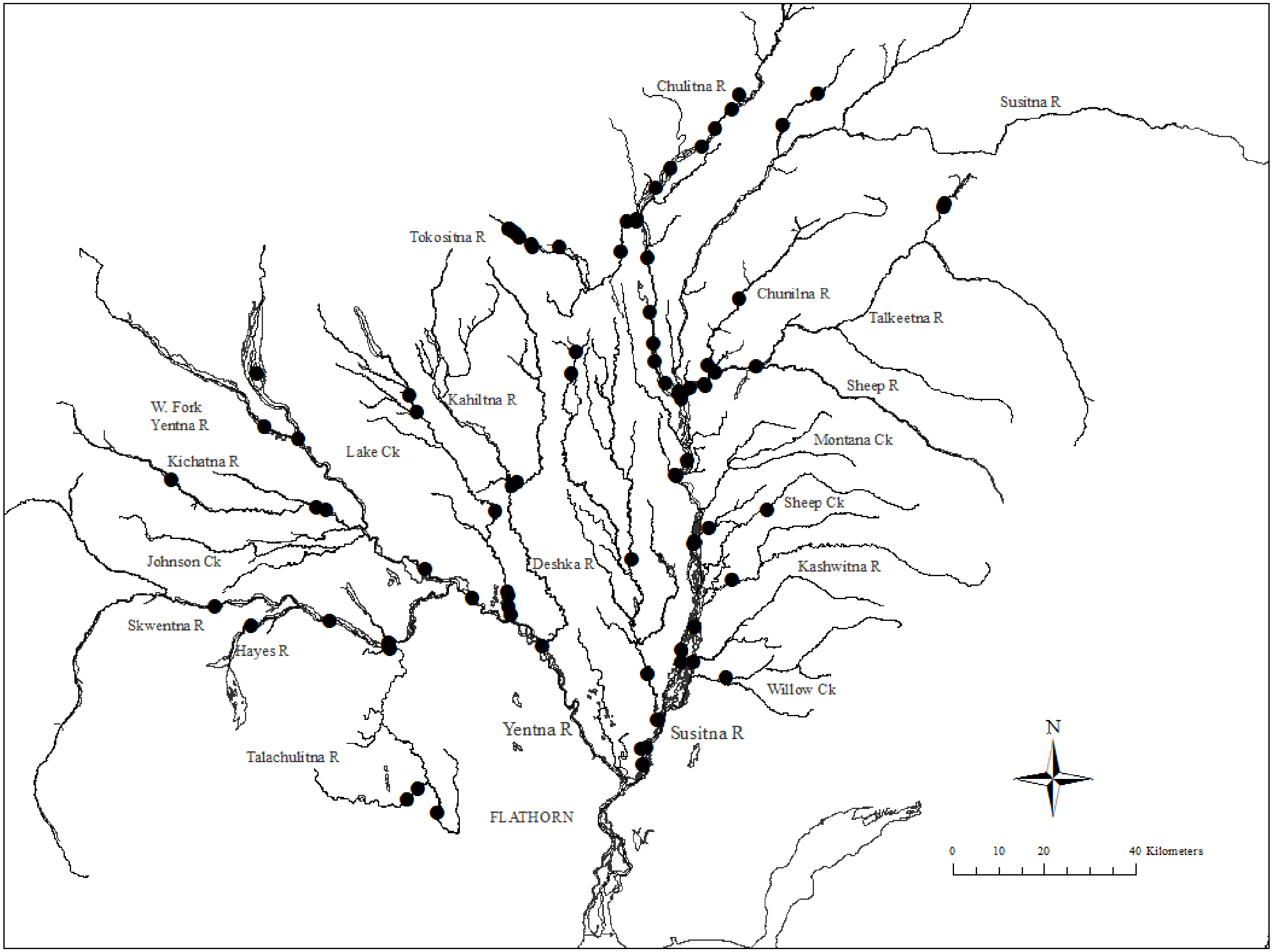

Figure 14.–Final locations of coho salmon radiotagged at FW 2, 2012.

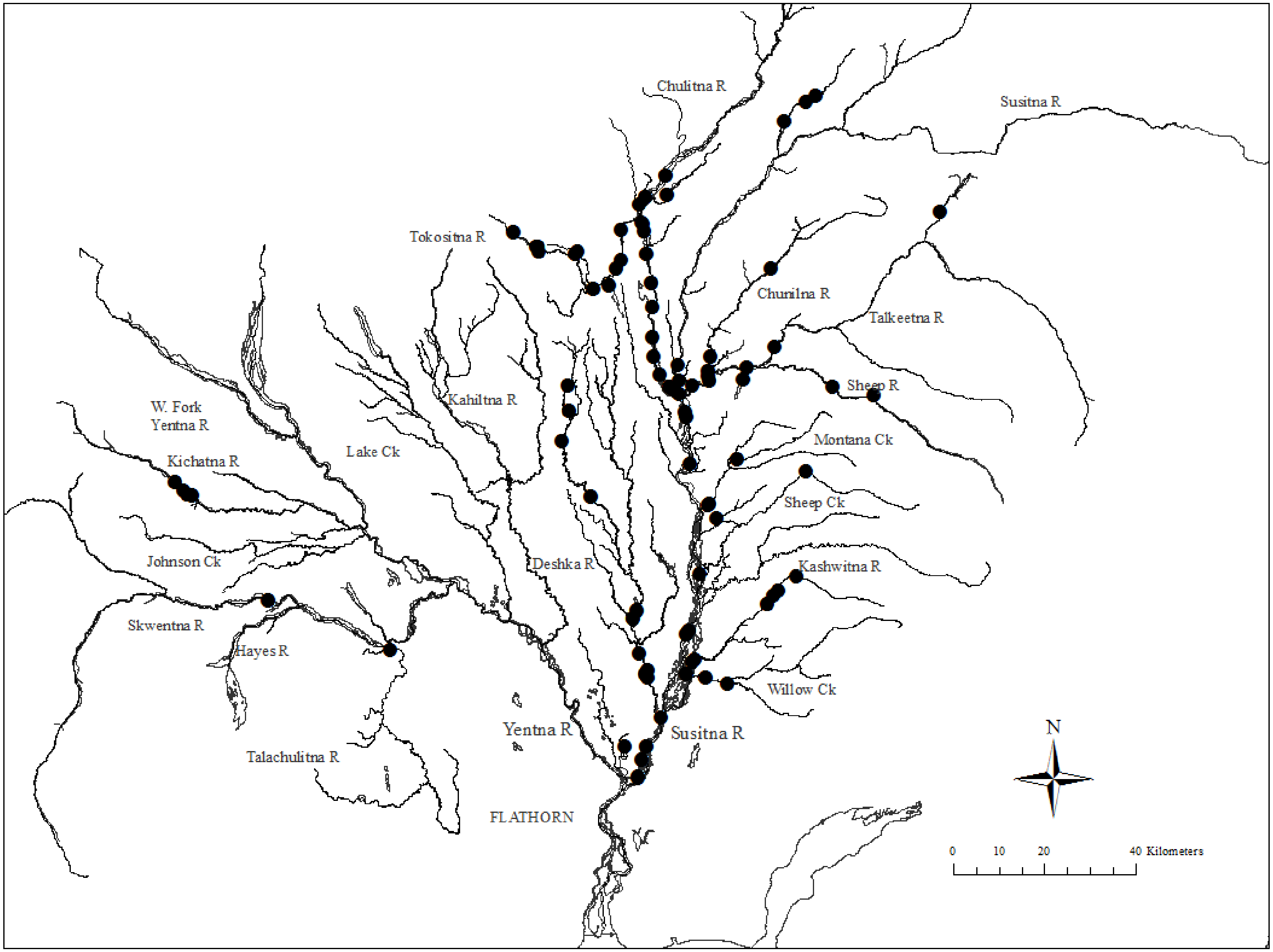

Figure 15.–Final locations of coho salmon radiotagged at FW 3, 2012.

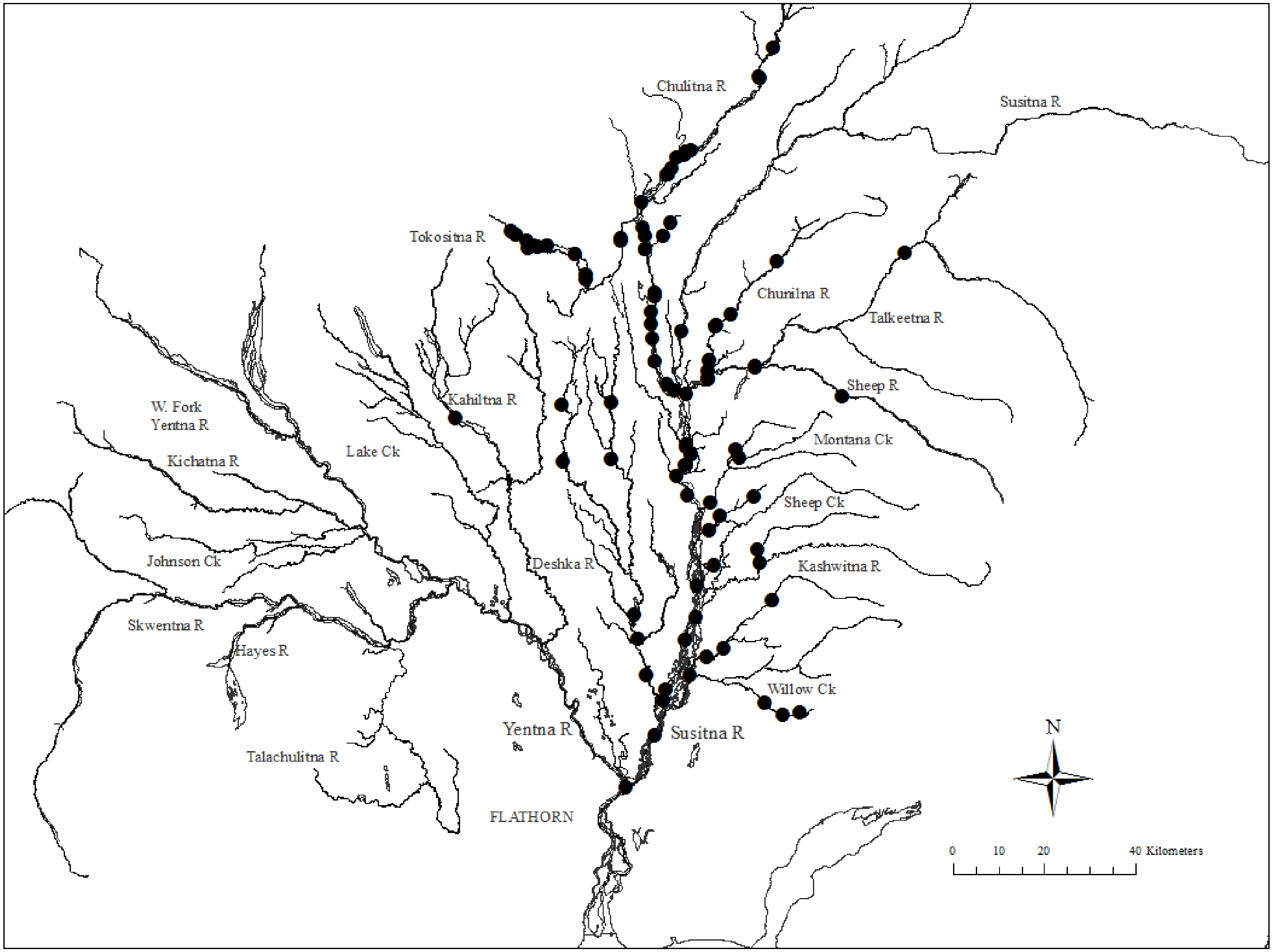

Figure 16.–Final locations of coho salmon radiotagged at FW 4, 2012.

Estimated Distribution of Spawning Salmon

Chum Salmon

Results from the mark–recapture experiment indicated that radio tags were not deployed in chum salmon proportional to passage over the course of the run. To estimate abundance of spawning salmon in different tributaries within the Susitna River drainage, the distribution of spawners was first estimated within each first-event stratum used in the mark–recapture model and then summed across all first-event strata. The estimated abundance of radiotagged chum salmon was effectively weighted by estimated passage within each first-event stratum (Table 13).

An estimated 229,903 (SE 155,193) chum salmon spawned in tributaries of the Susitna River above the mouth of the Yentna River in 2012. The number of chum salmon spawning in the Yentna River drainage in 2012 was estimated to be 99,442 (SE 84,876) fish (Table 14).

Table 13.–Estimated abundance, number of radio tags deployed, and relative weights (number of spawners per tag) used to estimate abundance within first-event strata for chum salmon spawning upstream from the Flathorn tagging site in the Susitna River, 2012.

First event stratum	Estimated abundance	Estimated SE	Radio tags deployed	Relative weight spawners/tag
Days 189–207	273,323	143,960	153	1,786.42
Days 208–210	14,580	10,096	43	339.06
Days 211–215	5,638	62,825	59	95.55
Days 116–219	13,662	7,726	27	505.99
Days 220–239	22,143	176,887	61	363.00

Table 14.–Chum salmon spawning distributions, based on weighted abundance (Table 13), in the Susitna River, 2012.

Location	Estimated abundance	SE	Intervals 95% lower	Intervals 95% upper
Susitna River above the Yentna River				
Susitna River mainstem RM 24–98	50,171	64,493	30,750	119,873
Deshka River	2,125	2,325	0	7,747
Eastside Susitna River	43,409	26,770	21,609	109,827
Talkeetna River	75,993	40,452	42,337	175,357
Susitna River mainstem and tributaries RM 98-154	24,097	18,234	11,858	59,821
Chulitna River	34,108	31,020	18,997	83,071
Total	229,903	155,193	143,362	528,890
Yentna River				
Yentna River mainstem				
Yentna R. mainstem below Skwentna R.	12,900	30,789	6,374	31,363
Yentna R. mainstem above Skwentna R.	9,609	11,614	3,984	23,875
Total	22,509	40,052	13,000	50,282
Kahiltna River	0	0	0	0
Lake Creek	4,977	7,950	788	14,574
Skwentna River	34,682	33,568	19,602	88,294
Talachulitna River	19,893	11,360	7,973	46,595
Upper Yentna Tributaries	17,381	11,267	6,685	44,782
Total	99,442	84,876	62,712	228,990

Coho Salmon

Results from the mark–recapture experiment indicated that radio tags were not deployed in coho salmon in proportion to passage over the course of the run. Radiotagged coho salmon were effectively weighted by estimated passage within each first-event stratum from the mark–recapture experiment (Table 15).

An estimated 90,397 (SE 36,701) coho salmon spawned in tributaries of the Susitna River above the mouth of the Yentna River in 2012. The number of coho salmon spawning in the Yentna River drainage in 2012 was estimated to be 93,919 (SE 10,688) fish (Table 16).

Table 15.–Estimated abundance, number of radio tags deployed, and relative weights (number of spawners per tag) used to estimate abundance within first-event strata for coho salmon spawning upstream from the Flathorn tagging site in the Susitna River, 2012.

First event stratum		Estimated abundance	Estimated SE	Radio tags deployed	Relative weight spawners/tag
FW 1	Days 189–212	75,437	11,871	59	1,278.59
	Days 213–216	4,925	3,851	11	447.74
	Days 217–239	8,221	3,113	19	432.71
FW 2–4	Days 189–214	88,924	38,074	196	453.70
	Days 215–217	3,738	2,722	25	149.51
	Days 218–239	3,071	4,360	45	68.25

Table 16.–Coho salmon spawning distributions, based on weighted abundance (Table 15), in the Susitna River, 2012.

Location	Estimated abundance	SE	Intervals	
			95% lower	95% upper
Susitna River above the Yentna River				
Susitna River mainstem RM 24–98	18,369	7,126	9,182	34,492
Deshka River	8,867	4,135	3,885	18,104
Eastside Susitna River	13,027	6,006	5,842	26,890
Talkeetna River	12,219	5,807	5,191	25,333
Susitna River mainstem and tributaries RM 98–154	2,872	1,688	693	6,817
Chulitna River	35,044	14,941	17,104	68,718
Total	90,397	36,701	46,672	173,872
Yentna River				
Yentna River mainstem				
Yentna R. mainstem below Skwentna R.	18,821	4,959	10,057	29,446
Yentna R. mainstem above Skwentna R.	12,119	3,719	5,744	20,272
Total	30,941	6,271	19,809	44,349
Kahiltna River	18,150	4,674	10,275	28,572
Lake Creek	8,254	3,078	3,460	15,407
Skwentna River	16,352	4,384	8,460	25,585
Talachulitna River	14,251	3,973	7,323	22,853
Upper Yentna Tributaries	5,971	2,469	1,841	11,413
Total	93,919	10,688	75,101	116,974

DISCUSSION

The 2012 Susitna River drainage spawning abundance estimates indicated approximately 70% (229,903/329,345) of chum salmon and 49% (90,397/184,316) of coho salmon migrated to areas in the Susitna River upstream of the Yentna River confluence (Tables 14 and 16). The remaining 30% of chum salmon and 51% of coho salmon migrated to the Yentna River drainage. It was assumed that radiotagged fish that migrated past the “gateway” Susitna Station tracking station ended their migration at spawning sites. However, verifying that radiotagged fish spawned was cost prohibitive and impractical because of turbid water conditions and a large geographic area. Putative spawning sites selected by chum and coho salmon in 2012 were similar to those selected in 2009 (Merizon et al. 2010) and 1981 (ADF&G 1981). Based on estimated abundances, approximately 53% (174,868/329,345) of chum salmon appeared to use main channel sites (Susitna, Yentna, and Skwentna rivers) versus 44% (81,561/184,316) of coho salmon (Tables 14 and 16). Few radiotagged chum salmon (4/371, 1.0%) were documented in the Kahiltna, Deshka, and Tokositna rivers. However, 20.8% (75/360) of radiotagged coho salmon were documented in these rivers (Table 12).

The diagnostic procedures for estimating abundance, as described in Appendix A2, indicated that probability of capture was not uniform over time or between marking sites (fish wheels) for both chum and coho salmon. Contingency table analyses recommended by Seber (1982) and described in Appendix A2 were used to detect significant temporal or geographic violations of assumptions of equal probability of capture.

The partially stratified model described by Darroch (1961) and used to estimate abundance for both chum and coho salmon allowed us to minimize bias in our estimates of abundance by accommodating heterogeneity in probability of capture (accompanied by lack of complete mixing) that was detected during both sampling events. The Darroch (1961) model also provided estimates of abundance for each temporal and geographic stratum for each sampling event. For the marking event, there were estimates of passage within each stratum. These estimates were used to weight each radiotagged fish for each first (marking) event stratum based on estimated passage and the number of radio tags deployed within each stratum. Estimates of spawning distribution were calculated based on these weighted observations of radiotagged fish, resulting in estimates of spawning distribution that were adjusted for variation in probability of capture when and where the radio tags were deployed. The imprecision or uncertainty in the weights is propagated through to our estimates of spawner distribution so that estimates of standard errors associated with spawner distribution reflect the uncertainty about these estimates.

This approach resulted in minimally biased estimates of both abundance and spawner distribution. Bias in these estimates may still exist due to our inability to detect all major sources of capture heterogeneity during the marking event, meaning the selected strata may not accurately compensate for that heterogeneity. However, the strata were selected based on known field conditions and supplemented and supported by the diagnostics tests for equal probability of capture described in Seber (1982).

As in the 2009–2011 radiotelemetry studies (Merizon et al. 2010; Cleary et al. 2013; Cleary et al. 2016), bank orientation (a stock-specific adult migration behavior) was present at the tagging fish wheels for both species (Figures 8–11 and 13–16). Although it would be best to position the fish wheels where bank orientation is not a concern, the Susitna River downstream of the Flathorn tagging site becomes braided, shallow, and subject to tidal influence. Therefore, it is unlikely that fish wheel sites could be located downstream that are suitable for capturing migrating chum and coho salmon prior to bank orientation behavior. The complete mixing condition required in a mark–recapture experiment could not be satisfied temporally in this system due to experimental design and the timing of movements of the fish being investigated.

The weighted abundance distribution determined for radiotagged coho salmon between the Yentna (49%) and Susitna (51%) rivers in 2012 is consistent with the weighted distributions determined for 2009 (43% and 56% in the Yentna and Susitna rivers, respectively; Merizon et al. 2010) and 2011 (39% and 61%, respectively; Cleary et al. 2016). In 2002, coho salmon were radiotagged in salt water in lower Cook Inlet, and the fraction, compared among 5 streams, did not differ, suggesting homogenous tagging is possible prior to fish entering the river (Willette et al. 2003).

The 1984–1985 and 2010–2012 chum and coho salmon mark–recapture projects were conducted using the Flathorn Site for tag deployment to estimate abundance. Based on these estimates, chum salmon run strength was greatest in 2011 (1,752,000), followed by 1984 (812,700 fish), 2010 (357,000), 2012 (329,300), and 1985 (316,800) (Table 17). Fish wheel mark–recapture coho salmon estimates were greatest in 2011 (216,600), followed by 2010 (196,000), 1984 (190,000), 2012 (184,000), and 1985 (77,000). In 2002, coho salmon abundance was estimated at 663,000 fish and was derived by radiotagging coho salmon in Cook Inlet (Willette et al. 2003) (Table 17).

A number of factors can affect the precision of abundance estimates. For fish wheel studies, these include variation in tag deployment and recovery methods, wheel design, changes in bottom structure at wheel sites, new locations of wheel sites, and water level effects on wheel speed. Like the mark–recapture studies conducted in the 1980s, 2010, and 2011, first-event data collected in 2012 for chum and coho salmon were collected at the Flathorn Site using fish wheels, and second-event data were collected upstream using fish wheels, one of which was at RM 6.2 on the Yentna River. However, unlike studies in the 1980s and in 2009, but similar to 2010 and 2011, fish wheels were operated in 2012 for tag-recovery at RM 34 on the lower Susitna River, downstream of previous tag-recovery sites at Sunshine (RM 80), Talkeetna (RM 103), and Curry (RM 120). In addition to tag recovery data collected at fish wheels during studies in the 1980s, tag data were also collected during surveys of steams and sloughs upstream of the deployment wheels.

Table 17.–Historical Susitna River chum and coho salmon abundance estimates.

		Site [a]			
Species	Year	Flathorn	Yentna	Sunshine	Mainstem Susitna
Chum salmon					
	1981	NA	19,800[b]	262,900	NA
	1982	NA	27,800[b]	430,400	NA
	1983	NA	10,800[b]	265,800	NA
	1984	812,700	26,500[b]	765,000	NA
	1985	316,800	NA	373,600	NA
	2010	357,000	202,000	NA	155,000
	2011	1,752,000	283,800	NA	1,468,200
	2012	329,300	99,400	NA	229,900
Coho salmon					
	1981	NA	17,000[b]	19,800	NA
	1982	NA	34,100[b]	45,700	NA
	1983	NA	8,900[b]	15,200	NA
	1984	190,100	18,200[b]	94,700	NA
	1985	77,400	NA	36,800	NA
	2002	NA	305,200	NA	358,000
	2010	196,000	136,000	NA	60,000
	2011	216,600	84,700	NA	131,900
	2012	184,300	93,900	NA	90,400

Source: 1981–1984 estimates from Barrett et al. (1985); 1985 estimates from Thompson et al. (1986); 2002 estimates from Willette et al. (2003); 2010 estimates from Cleary et al. (2013); 2011 estimates from Cleary et al. (*In prep*).

Note: NA means no attempt was made to estimate abundance.

[a] The Flathorn Site was located at Susitna River RM 22, the Yentna Site at Yentna River RM 6.2, the Sunshine Site at Susitna River RM 80, and the Mainstem Site at Susitna River RM 25.5.

[b] Side-scan sonar and fish wheel catch apportionment were used to estimate escapement.

The 2012 chum salmon estimate had poor precision (note SE in Table 14) because of a small number of recaptures and afforded inaccurate spawner distribution estimates (Table 13). Diagnostic tests for equal probability of capture indicated both temporal and geographic variation in probability of capture. Attempts to model both geographic and temporal probability of capture did not provide admissible abundance estimates. The model we used to produce the estimate in this report accounts for only temporal variation in probability of capture. We may have not captured all of the significant variability in probability of capture that was present during the 2012 chum salmon experiment, and our abundance estimate may be biased and low.

The radio telemetry study in 2002 estimated a run strength for Susitna River coho salmon that was greater than estimates of run strength for all other years (Table 17). However, the 2002 project did not collect data using fish wheels in the Susitna River. Instead, coho salmon were tagged in Cook Inlet using radio and passive integrated transponder tags and the marked fraction was estimated from radiotracking via aerial surveys. The radio tags were tracked after entering the Susitna River and used to apportion the coho salmon escapements among major drainages (Willette et al. 2003). Consequently, there is uncertainty when comparing estimates if methods are not consistent across studies and particularly when there are significant standard errors associated with an estimate or different possibilities for bias.

Stock assessment data have been collected for chum and coho salmon for many places in the Susitna River watershed (ADF&G 1981; Barrett et al. 1984; Hoffman and Crawford 1986; Thompson et al. 1986; Willette et al. 2003; Ivey et al. 2007). As this spawning distribution study continues in subsequent years and results become more refined and reliable, the historical data could be viewed in the context of the entire watershed to make it more useful. Additionally, this study provides genetic baseline samples to better define the stock composition of Susitna River chum and coho salmon runs. Such information could be useful to ADF&G when gauging land use, fishery management, or invasive species impacts to chum and coho salmon stocks.

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APPENDIX A: METHODS FOR DETECTING SIZE- OR SEX-SELECTIVE SAMPLING AND TESTS OF CONSISTENCY

Appendix A1.–Detection of size- or sex-selective sampling during a 2-sample mark–recapture experiment and its effects on estimation of population size and population composition.

Size-selective sampling

The Kolmogorov-Smirnov 2-sample test (Conover 1980) is used to detect significant evidence that size-selective sampling occurred during the first or second sampling events. The second sampling event is evaluated using the null test hypothesis of no difference by comparing the length frequency distribution of all fish marked during the first event (M) with that of marked fish recaptured during the second event (R). The first sampling event is evaluated by comparing the length frequency distribution of all fish inspected for marks during the second event (C) with that of R. A third test that compares M and C is then conducted and used to evaluate the results of the first 2 tests when sample sizes are small. Sample sizes are considered "small" if less than 30 for R and less than 100 for M or C.

Sex-selective sampling

Contingency table analysis (χ^2 test) is generally used to detect significant evidence that sex-selective sampling occurred during the first or second sampling events. The counts of observed males to females are compared between M and R, C and R, and M and C using the null hypothesis that the probability that a sampled fish is male or female is independent of the sample. If the proportions by gender are estimated for a sample (usually C), rather than observed for all fish in the sample, contingency table analysis is not appropriate and the proportions of females (or males) are then compared between samples using a 2-sample test (e.g., student's *t*-test).

Test outcomes	M vs. R	C vs. R	M vs. C	Result
Case I	Fail to reject H_o	Fail to reject H_o	Fail to reject H_o	No size or sex selectivity detected during either sampling event
Case II	Reject H_o	Fail to reject H_o	Reject H_o	No size or sex selectivity detected during the first event but there is during the second event
Case III	Fail to reject H_o	Reject H_o	Reject H_o	No size or sex selectivity detected during the second event but there is during the first event
Case IV	Reject H_o	Reject H_o	Either result possible	There is size or sex selectivity detected during both the first and second sampling events
Evaluation required:	Fail to reject H_o	Fail to reject H_o	Reject H_o	Sample sizes and powers of tests must be considered [a-d]

[a] If sample sizes for M vs. R and C vs. R tests are not small and sample sizes for M vs. C test are very large, the M vs. C test is likely detecting small differences that have little potential to result in bias during estimation. Case I is appropriate.

[b] If sample sizes for M vs. R are small, the *P*-value for M vs. R is not large (~0.20 or less), and sample sizes for C vs. R are not small or the *P*-value for C vs. R is fairly large (~0.30 or more), the rejection of the null in the M vs. C test was likely the result of size or sex selectivity during the second event, which the M vs. R test was not powerful enough to detect. Case I may be considered but Case II is the recommended, conservative interpretation.

[c] If sample sizes for C vs. R are small, the P-value for C vs. R is not large (~0.20 or less), and sample sizes for M vs. R are not small or the P-value for M vs. R is fairly large (~0.30 or more), the rejection of the null in the M vs. C test was likely the result of size or sex selectivity during the first event, which the C vs. R test was not powerful enough to detect. Case I may be considered but Case III is the recommended, conservative interpretation.

[d] If sample sizes for C vs. R and M vs. R are both small, and both P-values for C vs. R and M vs. R are not large (~0.20 or less), the rejection of the null in the M vs. C test may be the result of size or sex selectivity during both events, which the C vs. R and M vs. R tests were not powerful enough to detect. Cases I, II, or III may be considered but Case IV is the recommended, conservative interpretation.

-continued-

Case I
Abundance is calculated using a Petersen-type model from the entire data set without stratification. Composition parameters may be estimated after pooling length, sex, and age data from both sampling events.

Case II
Abundance is calculated using a Petersen-type model from the entire data set without stratification. Composition parameters may be estimated using length, sex, and age data from the first sampling event without stratification. If composition is estimated from second event data or after pooling both sampling events, data must first be stratified to eliminate variability in capture probability (detected by the M vs. R test) within strata. Composition parameters are estimated within strata, and abundance for each stratum needs to be estimated using a Petersen-type formula. Overall composition parameters are estimated by combining stratum estimates weighted by estimated stratum abundance according to the formulae below.

Case III
Abundance is calculated using a Petersen-type model from the entire data set without stratification. Composition parameters may be estimated using length, sex, and age data from the second sampling event without stratification. If composition is estimated from first event data or after pooling both sampling events, data must first be stratified to eliminate variability in capture probability (detected by the C vs. R test) within strata. Composition parameters are estimated within strata, and abundance for each stratum needs to be estimated using a Petersen-type formula. Overall composition parameters are estimated by combining stratum estimates weighted by estimated stratum abundance according to the formulae below.

Case IV
Data must be stratified to eliminate variability in capture probability within strata for at least 1 or both sampling events. Abundance is calculated using a Petersen-type model for each stratum, and estimates are summed across strata to estimate overall abundance. Composition parameters may be estimated within the strata as determined above, but only using data from sampling events where stratification has eliminated variability in capture probabilities within strata. If data from both sampling events are to be used, further stratification may be necessary to meet the condition of capture homogeneity within strata for both events. Overall composition parameters are estimated by combining stratum estimates weighted by estimated stratum abundance.

Stratification
If stratification by sex or length is necessary prior to estimating parameters, then an overall composition parameter (p_k) is estimated by combining within-stratum composition estimates using the following:

$$\hat{p}_k = \sum_{i=1}^{j} \frac{\hat{N}_i}{\hat{N}_\Sigma} \hat{p}_{ik} \text{ and} \tag{A1}$$

$$\hat{V}[\hat{p}_k] \approx \frac{1}{\hat{N}_\Sigma^2} \sum_{i=1}^{j} \left(\hat{N}_i^2 \hat{V}[\hat{p}_{ik}] + (\hat{p}_{ik} - \hat{p}_k)^2 \hat{V}[\hat{N}_i] \right) \tag{A2}$$

where

J = the number of sex or size strata,

$\hat{p}_{ik}$ = the estimated proportion of fish that were age or size *k* among fish in stratum *i*,

$\hat{N}_i$ = the estimated abundance in stratum *i*, and

$\hat{N}_\Sigma$ = sum of the $\hat{N}_i$ across strata.

Appendix A2.–Tests of consistency for the Petersen estimator (Seber 1982: page 438).

Of the following conditions, at least 1 must be fulfilled to meet assumptions of a Petersen estimator:

1) marked fish mix completely with unmarked fish between events
2) every fish has an equal probability of being captured and marked during event 1
3) every fish has an equal probability of being captured and examined during event 2

To evaluate these 3 assumptions, the chi-square statistic will be used to examine the following contingency tables as recommended by Seber (1982). At least 1 null hypothesis needs to be accepted for assumptions of the Petersen model (Bailey 1951, 1952; Chapman 1951) to be valid. If all 3 tests were rejected, a temporally or geographically stratified estimator (Darroch 1961) was used to estimate abundance.

I. Test for complete mixing

	Area or time where recaptured (second event strata)				Not recaptured
Area or time where marked	1	2	…	*t*	$(n_1\text{-}m_2)$ [a]
1					
2					
…					
s					

Note: This tests the hypothesis that movement probabilities (θ) from first event strata *i* (i = 1, 2, ...*s*) to second event strata *j* (j = 1, 2, ...*t*) are the same for all *i* within each *j*; H_0: $\theta_{ij} = \theta_j$.

[a] n_1 is the number captured in first event; m_2 is the number captured in the second event that were marked.

II. Test for equal probability of capture during the first event

	Area or time where examined (second event strata)			
	1	2	…	*t*
Marked (m_2)[a]				
Unmarked (n_2-m_2)[b]				

Note: This tests the hypothesis of homogeneity on the columns of this 2-by-*t* contingency table with respect to the marked to unmarked ratio among time or area designations; H_0: $\Sigma_i a_i\theta_{ij} = kU_j$ where θ_{ij} is the movement probability from first event strata *i* to second event strata *j*, *k* is the total marks released per total unmarked in the population, U_j is the total unmarked fish in stratum *j* at the time of sampling, and a_i is the number of marked fish released in time or area stratum *i*. For the Petersen estimator to be unbiased, *k* must equal total marks released per total unmarked in the population; this condition is satisfied if there is equal closure over tagging strata ($\Sigma_j\theta_{ij}$ = constant), i.e. the proportion of the run in each tagging stratum moving to inspected second event strata is the same for all tagging strata. The hypothesis can also be satisfied through mixing ($\theta_{ij} = \theta_{j\cdot}$) but because mixing is unlikely due to the experimental design, the test is one of equal probability of capture in the first event.

[a] m_2 is the number captured in the second event that were marked.

[b] n_2 is the number captured in the second event.

III. Test for equal probability of capture during the second event

	Area or time where marked (first event strata)			
	1	2	…	*s*
Recaptured (m_2)[a]				
Not recaptured (n_1-m_2)[b]				

Note: This tests the hypothesis of homogeneity on the columns of this 2-by-*s* contingency table with respect to recapture probabilities among time or area designations; H_0: $\Sigma_j \theta_{ij}p_j = d$ where θ_{ij} is the movement probability from time or area stratum *i* to section *j*, p_j is the probability of capturing a fish in section *j* during the second event, and *d* is a constant. The hypothesis can also be satisfied through mixing ($\theta_{ij} = \theta_{j\cdot}$), but because mixing is unlikely due to the experimental design, the test is one of equal probability of capture in the second event.

[a] m_2 is the number captured in the second event that were marked.

[b] n_1 is the number captured in the first event.