

**Fishery Data Series No. 02-28**

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**Inriver Abundance, Spawning Distribution, and  
Migratory Timing of Copper River Chinook Salmon  
in 2001**

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and  
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December 2002

Alaska Department of Fish and Game

Division of Sport Fish



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<b>Weights and measures (metric)</b>		<b>General</b>		<b>Mathematics, statistics, fisheries</b>	
centimeter	cm	All commonly accepted abbreviations.	e.g., Mr., Mrs., a.m., p.m., etc.	alternate hypothesis	$H_A$
deciliter	dL			base of natural logarithm	e
gram	g	All commonly accepted professional titles.	e.g., Dr., Ph.D., R.N., etc.	catch per unit effort	CPUE
hectare	ha	and	&	coefficient of variation	CV
kilogram	kg	at	@	common test statistics	F, t, $\chi^2$ , etc.
kilometer	km	Compass directions:		confidence interval	C.I.
liter	L	east	E	correlation coefficient	R (multiple)
meter	m	north	N	correlation coefficient	r (simple)
metric ton	mt	south	S	covariance	cov
milliliter	ml	west	W	degree (angular or temperature)	°
millimeter	mm	Copyright	©	degrees of freedom	df
<b>Weights and measures (English)</b>		Corporate suffixes:		divided by	÷ or / (in equations)
cubic feet per second	ft <sup>3</sup> /s	Company	Co.	equals	=
foot	ft	Corporation	Corp.	expected value	E
gallon	gal	Incorporated	Inc.	fork length	FL
inch	in	Limited	Ltd.	greater than	>
mile	mi	et alii (and other people)	et al.	greater than or equal to	≥
ounce	oz	et cetera (and so forth)	etc.	harvest per unit effort	HPUE
pound	lb	exempli gratia (for example)	e.g.,	less than	<
quart	qt	id est (that is)	i.e.,	less than or equal to	≤
yard	yd	latitude or longitude	lat. or long.	logarithm (natural)	ln
<b>Time and temperature</b>		monetary symbols (U.S.)	\$, ¢	logarithm (base 10)	log
day	d	months (tables and figures): first three letters	Jan,...,Dec	logarithm (specify base)	log <sub>2</sub> , etc.
degrees Celsius	°C	number (before a number)	# (e.g., #10)	mideye to tail fork	MEF
degrees Fahrenheit	°F	pounds (after a number)	# (e.g., 10#)	minute (angular)	'
hour (spell out for 24-hour clock)	h	registered trademark	®	multiplied by	x
minute	min	trademark	™	not significant	NS
second	s	United States (adjective)	U.S.	null hypothesis	$H_0$
<b>Physics and chemistry</b>		United States of America (noun)	USA	percent	%
all atomic symbols		U.S. state and District of Columbia abbreviations	use two-letter abbreviations (e.g., AK, DC)	probability	P
alternating current	AC			probability of a type I error (rejection of the null hypothesis when true)	$\alpha$
ampere	A			probability of a type II error (acceptance of the null hypothesis when false)	$\beta$
calorie	cal			second (angular)	"
direct current	DC			standard deviation	SD
hertz	Hz			standard error	SE
horsepower	hp			standard length	SL
hydrogen ion activity	pH			total length	TL
parts per million	ppm			variance	var
parts per thousand	ppt, ‰				
volts	V				
watts	W				

***FISHERY DATA SERIES NO. 02-28***

**INRIVER ABUNDANCE, SPAWNING DISTRIBUTION, AND  
MIGRATORY TIMING OF COPPER RIVER CHINOOK SALMON IN  
2001**

by

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## ABSTRACT

Radiotelemetry and mark-recapture techniques were used to estimate inriver abundance, spawning distribution, and migratory time-density functions of chinook salmon *Oncorhynchus tshawytscha* in the Copper River during 2001. Two-sample mark-recapture techniques were used to estimate inriver abundance. During the first sample, 22 May to 1 August, a total of 480 chinook salmon were captured, radio-tagged, and released downstream from the lower boundary of the Chitina subdistrict subsistence (CSS) fishery. The second sample, 4 June to 6 August, included 3,128 chinook salmon harvested from the CSS fishery, 425 chinook sampled from fish wheels and 75 sampled from dip nets in the Glennallen subdistrict subsistence (GSS) fishery, and 112 chinook captured in gillnets within the CSS fishery. Forty-five radio-tagged chinook salmon were recovered during the second sample. Estimated inriver abundance was 31,397 (SE=4,280) chinook salmon  $\geq 620$  mm MEF for the period 4 June-6 August. The estimate was expanded using the relationship between weekly abundance and CPUE from fishing during the first sample to account for the proportion of the run that passed prior to the opening of the CSS fishery on 4 June 2001. Total abundance was estimated to be 39,778 (SE=8,262) chinook salmon  $\geq 620$  mm MEF for the period 22 May-6 August.

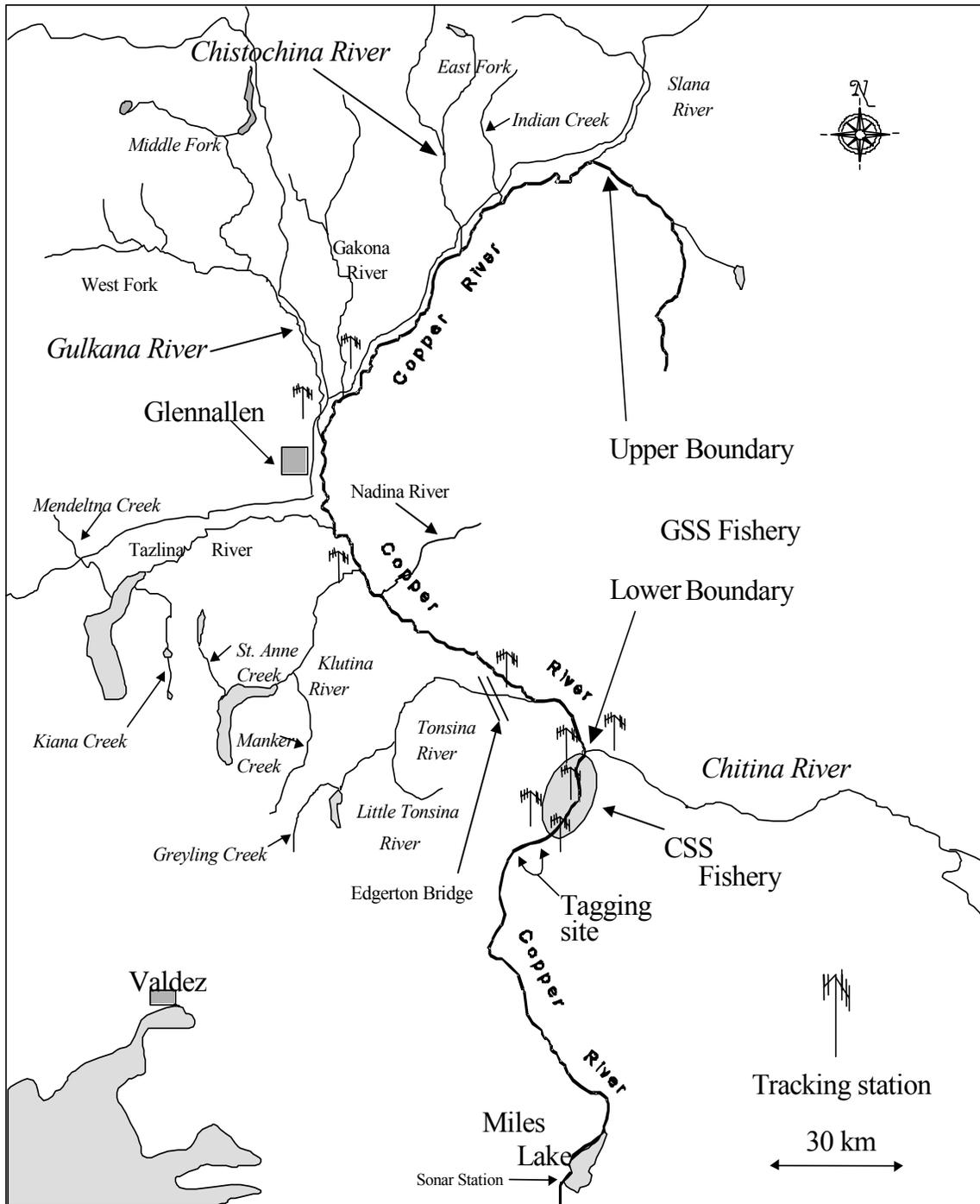
Two hundred ninety-three radio-tagged chinook salmon that migrated into tributary streams were used to determine the distribution of spawning chinook salmon. Estimated proportions of spawning chinook salmon by major drainage were, 0.26 for the Klutina River, 0.21 for the Tonsina River, 0.18 for the Gulkana River, 0.14 for the Chitina River, and 0.05 for each of the Tazlina and East Fork Chistochina rivers. Estimated proportions were similar to those estimated in 1999 and 2000, with the most fluctuation noted in the Gulkana (0.12-0.25) and Chitina (0.12-0.20) rivers. Mainstem spawners accounted for 0.82 of all chinook salmon in the Tonsina River and 0.67 of those in the Klutina River, which combined represented a substantial proportion (0.38) of the total escapement. The nine streams used for an aerial index of total escapement only accounted for 0.37 of chinook salmon migrating into spawning streams. The interannual variation in the proportion of the total escapement represented by these nine streams and the fact that a majority of these streams support stocks with early run timing patterns suggest that the aerial escapement index is neither a consistent nor reliable measure of total escapement.

Migratory time-density functions at the capture site varied among the major spawning stocks but remained relatively consistent from 1999-2001. In 2001, the mean date of passage varied from 2 June for chinook bound for the upper Copper River to 5 July for mainstem spawners in the Klutina River. In all three years of the study the migratory run-timing of chinook salmon bound for the tributaries of the Tonsina and Klutina rivers was earlier than their mainstem counterparts.

Key words: chinook salmon, *Oncorhynchus tshawytscha*, Copper River, East Fork Chistochina River, Gulkana River, Tazlina River, Klutina River, Tonsina River, Chitina River, abundance, mark-recapture, radiotelemetry, spawning distribution, aerial index, time-density functions.

## INTRODUCTION

From the large commercial fishery near Cordova, Alaska, to the inriver subsistence and recreational fisheries found in the upper Copper River Valley, the Copper River chinook salmon *Oncorhynchus tshawytscha* population supports a number of important fisheries. The total annual harvest of all fisheries from 1996 to 2000 averaged 68,540 chinook salmon (Taube and Sarafin 2001). The commercial fishery is prosecuted at the mouth of the Copper River and accounts for the largest proportion of the total annual harvest averaging 54,023 chinook salmon from 1996 to 2000. The subsistence fishery consists of the Chitina Subdistrict subsistence salmon (CSS) fishery, where fishers harvest migrating salmon with dip nets, and the Glenallen Subdistrict salmon (GSS) fishery, where fishers harvest salmon with fish wheels and dip nets (Figure 1). The average annual subsistence harvest from 1996 to 2000 was 7,317 chinook salmon. The recreational fisheries for chinook salmon primarily occur in two major tributaries, the Klutina and Gulkana rivers. The chinook salmon recreational fishery is the most important recreational fishery in the Copper River in terms of effort and economic value. The increase in tourism coupled with strong returns in recent years has led to a 27% increase in effort since 1988 (Taube and Sarafin 2001).



**Figure 1.-Map of the Copper River drainage demarcating the tagging site, boundaries of the Chitina and Glennallen subdistrict subsistence fisheries, and location of nine radio tracking stations, 2001.**

A limited understanding of returns, as well as the geographical and physical characteristics of the river, has made managing these fisheries difficult. Currently, the Copper River chinook salmon return is managed under a fixed escapement policy that is implemented through three management plans, where managers with the Alaska Department of Fish and Game (ADF&G) depend on in-season sonar counts, weekly anticipated harvest forecasts, and fishery-specific harvests to improve upon previous estimates of run strength. These management plans mandate ADF&G to manage the chinook salmon return so subsistence needs are met and escapements fall within the range 28,000-55,000 chinook salmon.

Estimates of abundance and total harvest of returning chinook salmon are required to manage Copper River chinook salmon fisheries under a fixed escapement policy. Harvest estimates are available for all fisheries, but historically, with the exception of a weir count in the Gulkana River in 1996 (LaFlamme 1997), aerial counts in select spawning tributaries have been the sole measure of chinook salmon spawning escapement. A total of 40 spawning streams have been identified throughout the drainage, but only nine are surveyed on a regular basis. The sonar at Miles Lake provides a total count of all salmon, but does not apportion the count between sockeye salmon *O. nerka* and chinook salmon. To ensure the escapement goal is met an accurate method for estimating the abundance of returning chinook salmon is required. This project completes the last year of a three-year (1999-2001) study assessing Copper River chinook salmon abundance, spawning distribution, and migratory timing.

## **OBJECTIVES**

The objectives of this study were to:

1. estimate the proportions of spawning chinook salmon in the Copper River in each major spawning tributary (Chitina, Tonsina, Klutina, Tazlina, Gulkana, and East Fork Chistochina rivers);
2. estimate the proportion of chinook salmon spawning in the nine tributaries assessed during aerial surveys in 2001 (Little Tonsina River, Greyling Creek, St. Anne Creek, Manker Creek, Mendeltna Creek, Kiana Creek, Gulkana River, East Fork Chistochina River, and Indian Creek); and,
3. estimate the inriver abundance of chinook salmon in the Copper River at the Chitina Subdistrict subsistence fishery.

Project tasks were to:

1. describe the stock-specific time-density functions at the entry point to the Chitina Subdistrict subsistence fishery, where stocks are defined as all chinook salmon spawning in the Chitina, Tonsina, Klutina, Tazlina, Gulkana, and Chistochina rivers; and,
2. determine the status of radio-tagged chinook salmon located in the mainstem Copper River immediately upstream of the Tonsina River during August as mortalities, migrating fish, or mainstem spawners.

## **METHODS**

### **STUDY DESIGN**

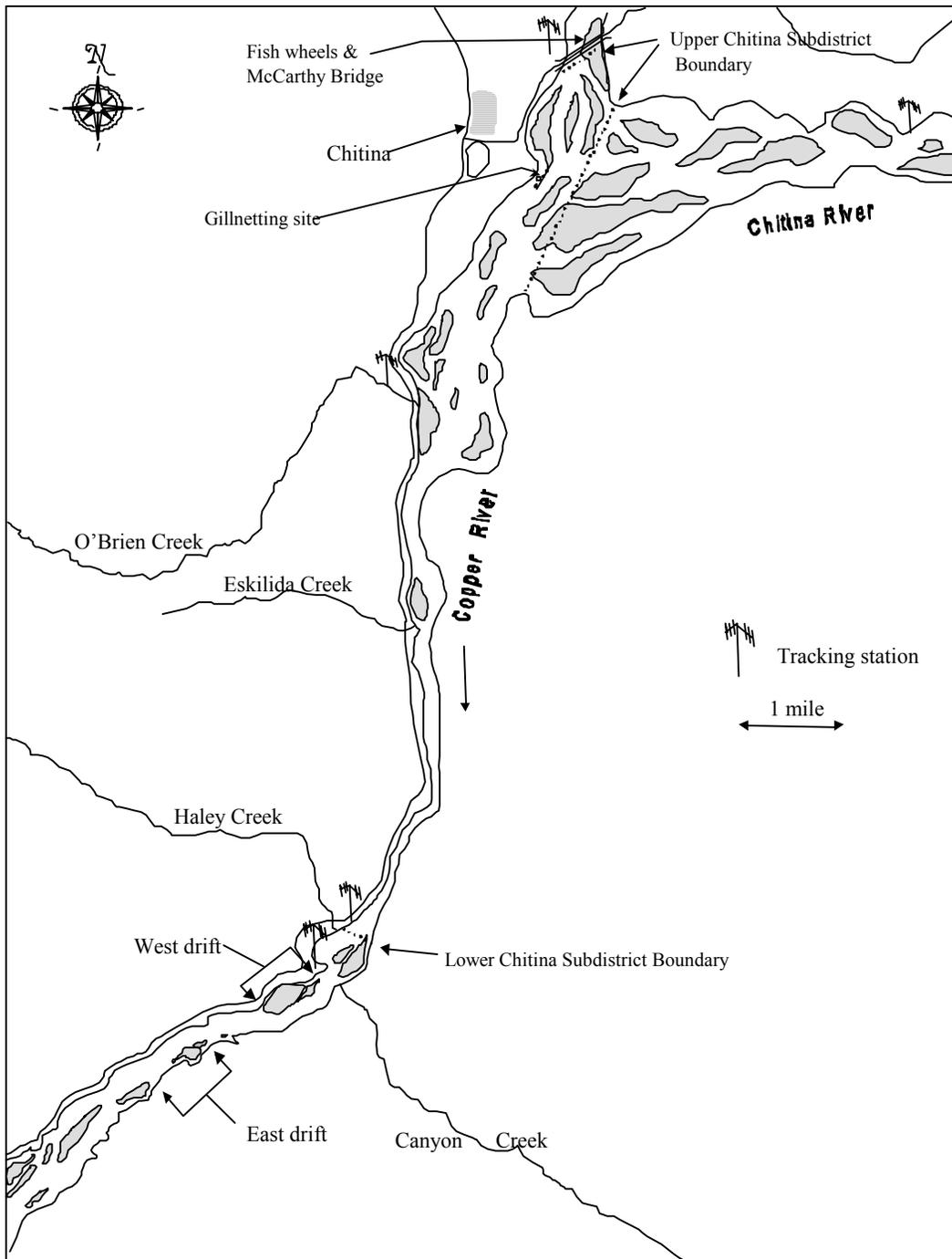
Inriver abundance, spawning distribution, and stock-specific time-density functions of Copper River chinook salmon in 2001 were estimated with a combination of radiotelemetry and mark-recapture methods. Two-sample mark-recapture techniques were used to estimate the inriver abundance. The first sample took place in the mainstem Copper River immediately downstream of the CSS fishery and involved marking chinook salmon with radio tags implanted through the esophagus. The second sample consisted of three components: 1) chinook salmon harvested in the CSS fishery from 4 June to 6 August; 2) chinook salmon captured with gillnets by ADF&G in the CSS fishery; and, 3) chinook salmon sampled from subsistence fish wheels catches located just upstream of the CSS fishery. Marked fish in the second sample were either sampled directly by ADF&G (fish wheel and gillnet catches), returned by CSS fishers, or were inferred as harvested in the CSS fishery by data collected at five automated radio tracking stations located within and on the boundaries of the fishery. The locations of the remaining marked salmon were determined with four additional tracking stations located throughout the drainage and by aerial and boat tracking surveys. The distribution of chinook salmon in the various spawning streams was estimated as the ratio of radio-tagged salmon migrating into a specific tributary to the total number of radio-tagged salmon surviving and migrating into all spawning tributaries. Stock-specific time-density functions at the entry point to the CSS fishery were determined with the date and time of initial capture.

### **CAPTURE AND TAGGING METHODS**

Chinook salmon were captured by drifting hand-held dip nets from a riverboat along two locations on the east and west banks of the Copper River approximately 1-3 km downstream from the lower boundary of the CSS fishery every day from 22 May to 1 August (Figure 2). Both east and west locations were fished by drifting downstream in waters along gravel bars with gradual slopes. At the start of each drift, a three person crew, consisting of a boat driver and two bow-positioned dipnetters, positioned the boat nearshore with the bow facing upstream. Dip nets were positioned vertically in the water column from the sides of the boat so the leading edge could be lightly placed on the bottom of the river. To ensure the dip nets remained open while drifting downstream the boat was idled slightly faster than the current of the river. Drift times and distance from shore were dependent on water levels but typically lasted 5 to 20 minutes and were conducted 3-10 m from shore.

Dip nets were commercially manufactured with rectangular-shaped (122 cm wide x 88 cm high) net heads constructed of solid-core aluminum tubing attached to tubular fiberglass handles (3-4 m long x 1.3 cm diameter). The attached net bags were constructed with knotted nylon (8.9-10.2 cm stretch measure) and were 1.3 m deep. Plastic shovel handles capping the fiberglass handles facilitated handling and allowed crew members to maintain orientation of the net head perpendicular to the direction of the drifting riverboat.

Immediately after capture, chinook salmon were placed in a holding tub to be sampled. Drifts were paused when a second chinook salmon was captured to avoid overcrowding in the holding tub. The boat was then anchored in a calm, backwater area where fish were measured to the nearest 5 mm MEF. Sex was determined from external characteristics. All fish received a uniquely numbered, gray spaghetti tag constructed of a 5-cm section of spaghetti tubing shrunk onto a 38-cm piece of 80-lb monofilament fishing line (Pahlke and Etherton 1999). The



**Figure 2.-Map of the study area for the mark-recapture experiment demarcating the capture and tagging location, upriver gillnet and fish wheel sampling sites, boundaries of the CSS fishery, and locations of five tracking stations, 2001.**

spaghetti tag was sewn through the musculature of the fish 1-2 cm ventral to the insertion of the dorsal fin between the third and fourth fin rays of the dorsal fin. Three scales were removed from the left side of the fish approximately two rows above the lateral line along a diagonal line downward from the posterior insertion of the dorsal fin to the anterior insertion of the anal fin (Welander 1940). Scale impressions were later made on acetate cards and viewed at 100X magnification using equipment similar to that described by Ryan and Christie (1976). Ages were determined from scale patterns as described by Mosher (1969).

Due to a limited number of radio tags available for deployment, not every captured fish received a radio tag. To ensure radio tags were deployed over the duration of the run, daily tagging rates were varied based on daily catch rates and historic run timing through the CSS fishery. Chinook salmon implanted with radio tags were supported in the holding tub while a radio tag was inserted through the esophagus and into the upper stomach using a 45-cm piece of polyvinyl chloride (PVC) tubing. The end of the PVC tube was slit lengthwise so the antenna end of the transmitter could be seated into the implant device. To gauge the distance of insertion into the fish, the implant device with the radio tag installed was placed alongside the fish and the distance from 1 cm posterior from the base of the pectoral fin to the tip of the snout was marked on the tube with the thumb of the person conducting the sampling. The radio tag was then seated into the upper stomach using a plunger, which was a second section of smaller diameter PVC tubing that fit through the center of the first tube. The entire handling process required approximately two to three minutes per fish.

Fishing effort was standardized to promote equal probability of capture of migrating chinook salmon. The protocol consisted of 2.5-h shifts twice each day, one between 0900 and 1300 hours and one between 1800 and 2300 hours. Fishing effort was alternated between the west and east banks every 45 minutes for the first 1.5 hours and every 30 minutes for the remainder of the shift. Fishing effort was measured as the time required to motor upstream to the start of a drift plus the time required to idle downstream to the end of a drift. The time required to sample fish or travel to the opposite bank were not included in the measurements of fishing effort.

## **RADIO-TRACKING EQUIPMENT AND TRACKING PROCEDURES**

Radio tags were Model Five pulse encoded transmitters made by ATS<sup>1</sup>. Each radio tag was distinguishable by its frequency and encoded pulse pattern. Fifty frequencies spaced approximately 20 kHz apart in the 149-150 MHz range with up to 10 encoded pulse patterns per frequency were used for a total of 500 uniquely identifiable tags available for deployment.

Nine stationary radio-tracking stations, similar to that described by Eiler (1995), were used to track migrating radio-tagged chinook salmon throughout the Copper River drainage (Figure 1). Each station included two 12 V marine deep cycle batteries, a solar array, an ATS model 5041 Data Collection Computer (DCC II), an ATS model 4000 receiver, an antenna switching box, a water-proof metal housing box, and a pair of four-element Yagi antennas (one aimed upstream and the other downstream). The receiver and data collection computer were programmed to scan through the frequencies at three-second intervals and both antennas received signals simultaneously. When a radio signal was encountered, the receiver paused for seven seconds, and the date, time, tag frequency, tag code, and signal strength for each antenna were recorded

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<sup>1</sup> Advanced Telemetry Systems, Isanti, Minnesota. Use of this company name does not constitute endorsement, but is included for scientific completeness.

by the data logger. Depending on the number of active tags in reception range, a full cycle through all 50 frequencies required 5-15 minutes. Data were downloaded onto a laptop computer every 7-10 days.

To maximize the chances of detecting all radio-tagged fish passing a site, tracking stations were placed in locations that provided an unobstructed view of the river. Two stations were placed on the west bank of the Copper River downstream from the CSS fishery. One was placed directly below the lower boundary marker, and the other approximately 500 m downstream. A third station was placed within the CSS fishery on a west-side bluff overlooking the Copper River at O'Brien Creek. A fourth station was placed on the north bank of the Chitina River approximately 6 km upstream from its confluence with the Copper River. A fifth station was placed on a west-side bluff overlooking the Copper River immediately upstream from the upper boundary of the CSS fishery (Figure 2). These five stations were used to identify all radio-tagged chinook salmon entering and exiting the CSS fishery. Tagged fish entering the Tonsina, Klutina, and Gulkana rivers were recorded by stations placed 1-5 km upstream from the mouths of the rivers. These three stations had negligible reception of transmitter signals in waters of the mainstem Copper River. A ninth station was placed on the mainstem Copper River approximately 2 km downstream from the mouth of the Gakona River (Figure 1). This station recorded signals from all radio-tagged fish bound for spawning areas upstream of the Gulkana River, collectively referred to as the Upper Copper River.

Aerial radio-tracking surveys were used to establish the distribution of radio-tagged chinook salmon throughout the Copper River drainage. Aerial surveys were conducted to locate radio-tagged chinook salmon in tributaries not monitored by the tracking stations, to locate fish that the tracking stations failed to record, and to validate whether fish recorded on the data loggers actually migrated into particular tributaries. Aerial surveys of Copper River tributaries upstream of the CSS fishery were conducted on 28-30 June, 24-27 July, and 21-22 August. During the final survey, a stretch of the Copper River below the tagging site was surveyed to locate radio tags that failed to enter the CSS fishery.

In addition to aerial surveys, boat surveys on the Copper River were used to define radio-tagged fish located in the mainstem river as mortalities, migrating salmon, or mainstem spawners. Two surveys were conducted on 8-9 and 14-17 August. The mainstem of the Copper River was surveyed from the mouth of the Nadina River downstream to the Chitina River and the Tonsina River was surveyed from the Edgerton Bridge downstream to the mouth (Figure 1). Radio-tagged fish were located by drifting downstream with a Yagi antenna attached to a 3-m wooden pole. The antenna was continually swept from one bank of the river to the other. Positions of located radio tags were recorded with a global positioning system (GPS) and radio tags located out of the water were retrieved when possible. Because the Copper River is extremely turbid with suspended glacial silt, areas where radio-tagged fish were located were examined for indicators of spawning activity. Freshly spawned-out carcasses or sightings of spawning activity (in shallow water or near the surface of the water) were considered evidence of mainstem spawning. To determine if radio tags located in the water were in live fish, the boat was driven directly over the area of the strongest signal. At this point, the radio tag was pinpointed again to determine if it had moved. After the river sections were initially surveyed, GPS locations of live fish from previous days were reexamined for indicators of spawning activity and to determine if the fish was still present and alive. On the final day of the survey, the Copper River from Haley

Creek to 2 km downstream from the capture site was surveyed to search for radio tags that failed to enter the CSS fishery.

The combination of location data from the tracking stations, aerial and boat surveys, tag return information, and upriver sampling was used to determine the final fate assigned to each radio tag (Table 1).

## **ESTIMATION OF INRIVER ABUNDANCE**

Two-sample mark-recapture techniques were used to estimate the inriver abundance of chinook salmon at the point of entry into the CSS fishery. Only chinook salmon given both a radio tag and a spaghetti tag were considered in the experiment. Tracking stations located at the lower boundary of the CSS fishery detected and logged all radio-tagged salmon entering the fishery. These fish constituted the marked fish for the first sample.

### **Second Sample: CSS Harvest and Upriver Sampling**

Upriver sampling activities coupled with the reported harvest from the CSS fishery constituted the second sample. The marked component of the second event consisted of radio-tagged chinook salmon observed during upriver sampling and radio-tagged fish harvested in the CSS fishery. Length and sex data from the CSS harvest and upriver sampling were collected as a means to test for selective sampling. CSS fishers returning tags were queried for information regarding date and location of capture. The CSS harvest was estimated from returned permits that required the subsistence fisher to record the total number of chinook salmon and the date they were harvested. CSS fishers were required to return or mail in their permits to an ADF&G office at the end of the season. Four letters were mailed out promoting fishers to capture their permits. Approximately 88% of fishers returned permits; however, for those fishers who did not return permits, harvest was estimated by modeling the trend in harvest for those fishers who returned permits. This estimate constituted only a small portion of the total harvest.

Upriver sampling consisted of sampling subsistence catches from fish wheels located near the McCarthy Road Bridge and sampling with gillnets in the CSS fishery (Figure 2). Upriver sampling was initiated to supplement the number of chinook salmon examined in the second sample because the bag limit of chinook salmon was reduced from four to one fish beginning in 2000. Subsistence fish wheels were sampled from 5-7 days per week from 2 June –18 July. Attempts were made to sample the majority of the subsistence harvest in the sampling area using two crew members working split-shifts to cover the greater part of the day. Gillnetting was conducted from 10-13, 20-21, and 25-28 June. A braided mono-filament gillnet was set at a single site approximately 2 km downstream of the McCarthy Road Bridge in the main river channel near the west bank. The gillnet measured 45.7 m long (25 fathoms) and was 29 panels deep. Two mesh panel sizes were used, and were either 18.3 cm (7.5 in) or 20.3 cm (8.0 in) stretch measure. Gillnets were fished 5 hours each day. Chinook salmon from all upriver sampling activities were measured to the nearest 5 mm MEF and the sex was determined from external characteristics. Scales for age determination were taken from the fish wheel and upriver samples to supplement the samples taken from the CSS fishery.

### **Conditions for a Consistent Estimator**

Mark-recapture experiments require certain conditions to be met before an estimate of abundance is accurate (Seber 1982). These conditions expressed in the circumstances of this study along with their respective design considerations, test procedures, and necessary adjustments for significant test results were that:

**Table 1.-List of possible fates of radio-tagged chinook salmon in the Copper River, 2001.**

Fate	Description
Radio Failure	A fish that was never recorded swimming upstream into the Chitina subdistrict subsistence fishery.
CSS Recapture <sup>a</sup>	A fish harvested in the Chitina subdistrict subsistence fishery.
Upriver Test Fishery Recapture <sup>a</sup>	A fish that was caught during upriver gillnetting or dipnetting.
Fish Wheel Recapture <sup>a</sup>	A fish that was caught in a fish wheel in the Glennallen subdistrict subsistence fishery and WAS sampled by ADF&G.
Subsistence Fishery Mortality	A fish harvested in the Glennallen subdistrict subsistence fishery upstream of the McCarthy Road bridge and WAS NOT sampled by ADF&G.
Sport Fishery Mortality	A fish harvested in one of the sport fisheries.
Spawner <sup>b</sup>	A fish that migrated through the CSS fishery and entered a spawning tributary of the Copper River.
Upstream Migrant	A fish that migrated upstream of the CSS fishery, was never reported as being harvested, and was either located only in the mainstem Copper River, or was never located anywhere after passing through the fishery.

<sup>a</sup> These radio-tagged fish constituted the marked fish in the second sample of the mark-recapture experiment.

<sup>b</sup> These radio-tagged fish were used to estimate spawning distribution and stock-specific migratory timing.

*Handling and tagging did not make a fish more or less vulnerable to capture in the second sample than untagged fish.*

Design Considerations: Holding time of captured fish was kept to a minimum. Obviously stressed fish (fish placed in the holding tank that were slow to recover from capture) or injured fish were not tagged. The time required for radio-tagged fish to move from the capture site to the lower boundary of the fishery as well as transit times through the CSS fishery were calculated from information recorded by the tracking stations.

Test: There was no explicit test for this assumption because we could not observe the behavior of unhandled fish. However, we compared recapture rates and migration rates between groups of fish affected differently by handling, as reflected in the time required to recover from handling and reach the lower boundary of the CSS fishery. Groups were defined as those fish that required 2 days or less, 2-7 days, or greater than 7 days to recover from tagging and migrate into the fishery. If recapture rates and transit times through the CSS fishery were similar for the different groups, we interpreted this to mean that the effect of handling on tagged fish had abated by the time the fish reached the CSS fishery.

Adjustment: If recapture rates and/or migratory behavior appeared to be related to relative to handling effect, and if handling effect and fish size were not related, abundance would be estimated after removing fish severely affected by handling (e.g. 7-day recovery) from the marking and examination events. The number of fish affected severely would later be added to the estimate. If handling effect and fish size were related, the population would be stratified by size and this procedure would be repeated for each size stratum.

*There was no selection for tagged fish harvested in the CSS fishery.*

Design considerations: To reduce the likelihood of CSS fishers selecting for radio-tagged fish there was no reward for tag returns and gray spaghetti tags were used to reduce the probability of a fisher easily identifying a tagged fish. Gray tags are less identifiable at the time of capture but are easily identifiable when processing a fish. Selection for tagged fish would result in an estimate of abundance that would be biased low.

Test: There was no explicit testing procedure for tag selection. However, we believe the combination of tag color and no reward discouraged fishers from selecting radio-tagged salmon.

*All tagged fish harvested in the CSS fishery were accurately reported.*

Design considerations: Tag recoveries were obtained through on-site creel sampling and by voluntary tag returns. Tag recovery forms and instructions for data collection were sent to ADF&G offices in Fairbanks, Delta Junction, Glennallen, Cordova, Palmer, and Anchorage. Informational bulletins were posted at these offices and at strategic positions in and around the CSS fishery. Informational cards encouraging tag returns were distributed with CSS permits issued at ADF&G offices. All radio tags were labeled with information to encourage reporting of harvested tags. If either the radio or spaghetti tag from a harvested fish was not returned, attempts were made to contact the CSS fisher to determine if the fish was harvested (as opposed to the tag being removed and the fish released) and if both tags were attached. Tags that were harvested in the CSS fishery but not reported were identified using the tracking stations located at O'Brien and Haley Creeks. Radio tags removed from the water have a pronounced increase in signal strength compared to tags that are in the

water. Criteria for declaring an unreported tag as harvested were: 1) a pronounced and prolonged recording of a signal by a data logger at O'Brien and/or Haley Creek; 2) the radio tag was never recorded or located upstream of the CSS fishery; and, 3) no downstream movement of the radio tag was detected by the tracking station located below Haley Creek after the radio tagged fish had entered the CSS fishery.

*Tagged fish did not lose their tags, and there was no mortality of tagged fish between the tagging site and the CSS fishery.*

Design Considerations: Two tracking stations were placed at the lower end of the CSS fishery. All fish were double marked with radio tags and individually numbered spaghetti tags. Both tags were requested from CSS fishers. When only one tag was returned, a follow up telephone call was made to find out if the other tag was present.

Adjustment: All radio-tagged fish that did not migrate past the lower tracking stations were removed from the marked sample.

*Marked fish mixed completely with unmarked fish across the river and no fish had a zero probability of capture.*

Design Considerations: Because sampling in the test fishery and fishing in the CSS fishery was bank-oriented, fish swimming in center of the river may not have been included in the estimate. Because both banks of the river were sampled during both events, mixing of tagged fish between banks was investigated. Bank of capture for all fish was recorded and bank of recapture was requested from CSS fishers. Bank of capture for unmarked fish in the second sample (from the CSS fishery) was not known.

Test: Recapture rates for fish marked on each bank were compared using contingency  $\chi^2$  test analysis. Independence between bank of mark and bank of recapture was also tested.

Adjustment: If there was a center-only segment of the run, the estimate would be biased low and not include the unknown fraction of the population that migrated up the center of the river outside of the sampled areas. No adjustment or test was possible for this condition. However, if marked fish crossed-over between samples, it was inferred that fish not subject to capture in the first event because they were in the center of the channel would at some point swim near shore in the CSS fishery and be vulnerable to capture in the second event. If there was cross-over between sampling events, but the marked fraction was different for the two banks, a geographically stratified estimator such as the method of Darroch (1961) would be used to estimate abundance. If there was no cross-over between sampling events, a stratified Petersen model would be used to estimate abundance.

*Fish had equal probabilities of being marked or equal probabilities of being recaptured regardless of their size or sex.*

Design Considerations: dip nets, which are efficient at capturing all sizes of chinook salmon, were used in the first event. Sex and length were recorded for all tagged fish. In the second event, age, sex and length data were collected from a sample of fish harvested from the CSS fishery, and from those fish captured during upriver gillnet and fish wheel sampling.

Test: To investigate the possibility of sex-selective sampling by gear, we used a  $\chi^2$  test to compare the number of males and females that were recaptured and not recaptured. If this

test indicated a significant bias, the following tests would be done for males and females separately. If the test did not indicate a significant bias, males and females would be combined and Kolmogorov-Smirnov (K-S) two-sample tests ( $\alpha = 0.1$ ) for equal capture probabilities on cumulative length distributions of: Test A) all fish marked during the first sampling event and tagged fish recaptured in the second event; and, Test B) all fish marked during the first sampling event and all fish sampled in the second event would be performed. The null hypothesis was no difference between the distributions of lengths for Test A or for Test B. For these two tests there were four possible outcomes:

Case I: Accept  $H_0(A)$ , Accept  $H_0(B)$ . There was no size-selectivity during the first sampling event (when fish were marked) or during the second sampling event (when fish were harvested).

Case II: Accept  $H_0(A)$ , Reject  $H_0(B)$ . There was no size-selectivity during the second sampling event but there was size-selectivity during the first sampling event.

Case III: Reject  $H_0(A)$ , Accept  $H_0(B)$ . There was size-selectivity during both sampling events.

Case IV: Reject  $H_0(A)$ , Reject  $H_0(B)$ . There was size-selectivity during the second sampling event; the status of size-selectivity during the first event was unknown.

Adjustment: Depending on the outcome of the tests, one of the following procedures was used to estimate the abundance of the population:

If the test comparing recapture rates by sex was significant, a stratified estimate of abundance would be estimated for each sex and the two estimates would be added to estimate total abundance. Results of the tests comparing length distributions would dictate one of the following procedures to estimate abundance.

Case I: An unstratified estimate of abundance would be calculated. Lengths, sexes, and ages from both sampling events would be pooled to improve precision of proportions in estimates of compositions.

Case II: An unstratified estimate of abundance would be calculated, and only lengths, sexes, and ages from the second sampling event would be used to estimate proportions in compositions.

Case III: Both sampling events would be stratified, and abundance would be estimated for each stratum. The estimates of abundance would be added across strata to get a single estimate for the population. Lengths, ages, and sexes from both sampling events would be pooled to improve precision of proportions in estimates of composition.

Case IV: Both sampling events would be stratified and abundance estimated for each stratum. The estimates of abundance would be added across strata to get a single estimate for the population. Also, a single estimate of abundance would be calculated without stratification.

Case IVa: If the stratified and unstratified estimates of abundance for the entire population were dissimilar, the unstratified estimate would be discarded. Only lengths, ages, and sexes from the second sampling event would be used to estimate proportions in composition.

Case IVb: If the stratified and unstratified estimates of abundance for the entire population were similar, the estimate with the larger variance would be discarded. Only lengths, ages, and sexes from the first sampling event would be used to estimate proportions in compositions.

*Fish had equal probabilities of being marked regardless of time of capture.*

Design Considerations: Near equal fishing effort was expended at all times during the first event. Attempts were made to radio tag chinook salmon proportional to daily catch in the test fishery. Date and time of capture for all fish were recorded.

Test: Marked to unmarked ratios in the second event was compared among weeks to evaluate if this condition was met. Testing of this assumption required temporal harvest data from the CSS fishery. Temporal harvest data were available from most returned CSS fishery permits. The estimated harvest from unreported permits and reported permits without date of capture information was assigned to temporal strata in proportion to the distribution of the actual reported harvest.

Adjustment: If the condition was not met, then the condition that marked fish had equal probabilities of being recaptured regardless of when they entered the fishery was examined.

*Marked fish had equal probabilities of being recaptured regardless of when they entered the fishery.*

Test: Equal catchability was tested by comparison of recapture rates by week of entry into the CSS fishery using  $x^2$  test analysis.

Adjustment: If both recapture rates (this test) and marked:unmarked ratios (previous test) differed significantly over the various periods, a temporally stratified estimator such as the method of Darroch (1961) would be used. Consecutive strata having similar recapture rates would be pooled.

### **Estimator**

The Chapman modification of the Petersen two-sample model was used to estimate abundance (Seber 1982). The estimate was germane to the point of entry into the CSS fishery (prior to any inriver harvest of chinook salmon). Because some chinook salmon were tagged and migrated through the CSS fishery prior to its opening, and because no tagged fish were recaptured until 4 June, the estimate only pertained to the period 4 June – 6 August. The estimate was calculated using:

$$\hat{N} = \frac{(M+1)(\hat{C}+1)}{R+1} - 1 \quad (1)$$

$$V[\hat{N}] = \frac{(M+1)(\hat{C}+1)(M-R)(\hat{C}-R)}{(R+1)^2(R+2)} \quad (2)$$

where:

$\hat{N}$  = estimated abundance of chinook salmon from 2 June to 30 July;

M = the number of chinook salmon radio tagged during the first sampling event;

$\hat{C}$  = the estimated number examined during the second sampling event; and,

R = the number of radio-tagged chinook salmon captured during the second event.

The estimated variance of  $\hat{N}$  is approximate because  $\hat{C}$  was estimated from returned CSS permits. Because the estimate of CSS harvest was very precise (CV < 0.1%), the sampling error in  $\hat{C}$  was considered negligible.

To estimate the total inriver chinook salmon run, including those portions of the run that passed through the CSS fishery before the recovery event began (4 June),  $\hat{N}$  was multiplied by the inverse of the estimated proportion of the run  $\hat{P}$  that passed by the capture sites between 4 June and 6 August:

$$\hat{N}' = \hat{N}\hat{P}^{-1} \quad (3)$$

$$\text{var}(\hat{N}') = \hat{N}^2 \text{var}(\hat{P}^{-1}) + (\hat{P}^{-1})^2 \text{var}(\hat{N}) - \text{var}(\hat{P}^{-1}) \text{var}(\hat{N}). \quad (4)$$

The method for estimating  $\hat{P}^{-1}$  and its variance used weekly estimates of abundance in the CSS fishery from a Darroch (1961) capture-recapture model with weekly cumulative CPUE data for the weeks of the fishery to model the uncertainty with which CPUE predicted salmon abundance during the fishery. Markov-chain Monte Carlo (MCMC) methods were used to perform a Bayesian analysis (Carlin and Louis, 2000) of the relationship between weekly abundance and CPUE, which was used, in turn, to estimate fish abundance for weeks of the run outside the fishery. The estimate  $\hat{P}^{-1}$  and its variance were calculated from the 500,000 MCMC samples drawn from its posterior distribution:

$$\hat{P}^{-1} = \frac{\sum_{i=1}^S \tilde{P}_i^{-1}}{S} \quad \text{and} \quad \text{var}(\hat{P}^{-1}) = \frac{\sum_{i=1}^S (\tilde{P}_i^{-1} - \hat{P}^{-1})^2}{S} \quad (5)$$

where:

S = the number of Monte Carlo draws; and,

$\tilde{P}_i^{-1}$  is the value of the expansion factor for the  $i$ th draw. Each  $\tilde{P}_i^{-1}$  was calculated:

$$\tilde{P}_i^{-1} = \frac{\sum_{j \in B} \tilde{N}_{ij} + \sum_{j \in D} N_j^* + \sum_{j \in A} \tilde{N}_{ij}}{\sum_{j \in D} N_j^*} \quad (6)$$

where:

$N_j^*$  are weekly estimates of numbers of salmon in the recovery area using a time stratified Darroch (1961) estimation procedure with the capture-recapture data;

$\tilde{N}_{ij}$  is the projected number of salmon in the recovery area during week  $j$  in the  $i$ th simulation; and,

B, D, and A are the weeks before, during, and after the second (recovery) event.

To calculate the  $\tilde{N}_{ij}$  the WINBUGS software package (Spiegelhalter et al. 1996) was used to simulate the posterior distribution of the parameters in the following model, given the data  $j \in D$ ,

$$N_j^* = \beta * CPUE_j + \epsilon_j \text{ where } \epsilon_j \sim N(0, \mathbf{D} \sigma^2) \quad (7)$$

where  $\mathbf{D}$  is a diagonal matrix representing any heteroskedasticity in the variance structure. The MCMC posterior distribution for  $\hat{\beta}$  was used to generate the necessary projections:

$$\tilde{N}_{ij} = \hat{\beta}_i * CPUE_j. \quad (8)$$

## DISTRIBUTION OF SPAWNERS

All radio-tagged fish located in a spawning area (“spawner” fate in Table 1) were assigned to one of six major tributaries: the Chitina, Tonsina, Klutina, Tazlina, and Gulkana rivers, or upper Copper River drainage. The upper Copper River drainage was defined as all tributaries upstream of the Gulkana River.

The daily radio tagging rate and hours of fishing effort ( $h_i$ ) in the first sample varied by day. The count of fish tagged on day  $i$  having fate  $j$  ( $R_{ij}$ ) was adjusted by dividing by  $h_i$  and the tagging rate  $\left(\frac{x_i}{X_i}\right)$  where  $x_i$  is the number of fish radio tagged and  $X_i$  is the total number of chinook salmon caught on day  $i$ . The adjusted count was

$$Y_{ij} = \left(\frac{X_i}{h_i x_i}\right) R_{ij}. \quad (9)$$

Among fish that migrated upstream of the capture site, the proportion of fish that had spawning fate  $j$  was estimated as

$$\hat{P}_j = \frac{\sum_i^{\text{days}} Y_{ij}}{\sum_j \sum_i Y_{ij}}. \quad (10)$$

Variance was estimated using bootstrap resampling techniques (Efron and Tibshirani 1993). All radio tags were assigned a numeric weight that accounted for the daily tagging rate and fishing effort. In addition, all radio-tagged fish assigned spawner fates were further categorized with spawning fates (e.g. Gulkana River spawner). Each bootstrap replicate drew a random sample of

480 fates (total number of radio tags deployed) and their corresponding weights. From each replicate the proportion of spawners with spawning fate  $j$  was calculated for a total of 1,000 bootstrap data sets. The percentile method was used to estimate confidence intervals.

The same procedure was used to determine the proportion of chinook salmon spawning in the nine aerial index survey streams: Little Tonsina River, Grayling Creek, St. Anne Creek, Manker Creek, Mendeltna Creek, Kiana Creek, Gulkana River, East Fork Chistochina River, and Indian Creek. A chinook salmon was assigned to a index stream if the fish was located in that stream at least once during the aerial surveys.

### MIGRATORY TIMING

Migratory timing patterns were described as time-density functions, where the relative abundance of a particular stock  $t$  that entered into the fishery during time interval  $i$  was considered discrete and is described by Mundy (1979) as:

$$f(t_i) = \frac{m_i}{m} \quad (11)$$

where:

$f(t_i)$  = the empirical probability distribution over the total span of the run for fish spawning in tributary  $t$ ;

$m$  = the total number of radio-tagged chinook salmon that ended up in tributary  $t$ ; and,

$m_i$  = the subset of  $m$  radio-tagged chinook salmon bound for tributary  $t$  that were caught and tagged during the  $i^{\text{th}}$  day.

For this analysis, stocks were defined as all chinook salmon spawning in the Chitina, Tonsina, Klutina, Tazlina, and Gulkana rivers, and the upper Copper River drainage. Those fish assigned a fate of spawner (Table 1) were used to determine the time-density functions.

The mean date of passage ( $\bar{t}$ ) into the CSS fishery for a spawning stock was defined as:

$$\bar{t} = \sum_{i=1}^{\ell} t_i f(t_i). \quad (12)$$

The variance of the run timing distribution was defined as:

$$s^2 = \sum_{i=1}^{\ell} (t_i - \bar{t})^2 f(t_i) \quad (13)$$

where:

$t_i$  = time interval  $i$ ; and,

$\ell$  = the number of time intervals (days) during the total span of the run.

## RESULTS

### CAPTURE AND TAGGING

Five hundred ninety-six chinook salmon were captured during the first sample. The first fish was captured on 23 May and the last on 1 August. Four hundred eighty chinook salmon were tagged with both spaghetti and radio tags while the remaining 116 fish received only spaghetti tags. The largest daily CPUE of chinook salmon was 8.3 fish per hour on 2 June. The daily radio tagging rate varied from 0.5 to 1.0 tags per fish caught and generally tracked the daily catches (Figure 3).

### SECOND SAMPLE: CSS FISHERY HARVEST AND UPRIVER SAMPLING

Total harvest in the CSS fishery in 2001 was 3,107 (SE = 25) chinook salmon. The estimated harvest from 4 June-6 August was 3,016 chinook salmon. During that period, CSS fishers reported a harvest of 2,721 chinook salmon and the harvest estimate for fishers not returning permits was 295 (SE=24). Also during the second sample, 425 chinook salmon were examined in GSS fishery fish wheels, 75 were sampled from GSS fishery dip nets, and 112 were sampled from gillnets.

### FATES OF RADIO TAGGED CHINOOK SALMON

Four hundred thirty-seven of 480 radio-tagged chinook salmon entered the CSS fishery (Table 2). Forty-five tags were recovered in the second sample. Thirty-five of these were harvested by CSS fishers, nine were sampled from fish wheels, and one was recovered from gillnet sampling. Thirty of the 35 tags harvested by CSS fishers were returned. The five radio-tagged fish not reported were assumed to be harvested based on strong signal strength recordings at the O'Brien (mid-fishery) and Haley Creek (lower boundary) tracking stations, which implied the radio tags were removed from the water.

Three hundred seventy-seven radio-tagged chinook salmon migrated through the CSS fishery. Twenty-five of these fish were never reported as harvested or located in a spawning tributary, 16 were harvested in subsistence fish wheels (other than those sampled by ADF&G), 10 were harvested in sport fisheries, and 293 were located in spawning areas (Table 2). All radio-tagged fish were located at least once by one of the tracking stations or during boat and aerial tracking surveys (Table 3).

### INRIVER ABUNDANCE: TESTS OF CONSISTENCY

The probability of capture for chinook salmon in the CSS fishery did not appear to be altered by tagging or handling techniques. The tracking stations located at the lower end of the CSS fishery detected nearly 70% of radio-tagged fish within two days of capture and less than 6% required ten days or more (Figure 4). In addition, the majority of radio-tagged fish entering the CSS fishery migrated through the fishery in less than five days (Figure 4). Transit times through the CSS fishery were similar between fish that displayed minimal (less than 2 d), moderate (2-7 d), and substantial (greater than 7 d) delays between time of capture and entry into the CSS fishery (Figure 4). Furthermore, recapture rates were independent of the amount of time fish were delayed in migrating upstream (Table 4;  $\chi^2=2.92$ ;  $df=2$ ,  $P=0.23$ ).

There was no tag loss or natural mortality between the first and second samples. Forty-three of 480 radio-tagged chinook salmon were removed from the study because they never entered the

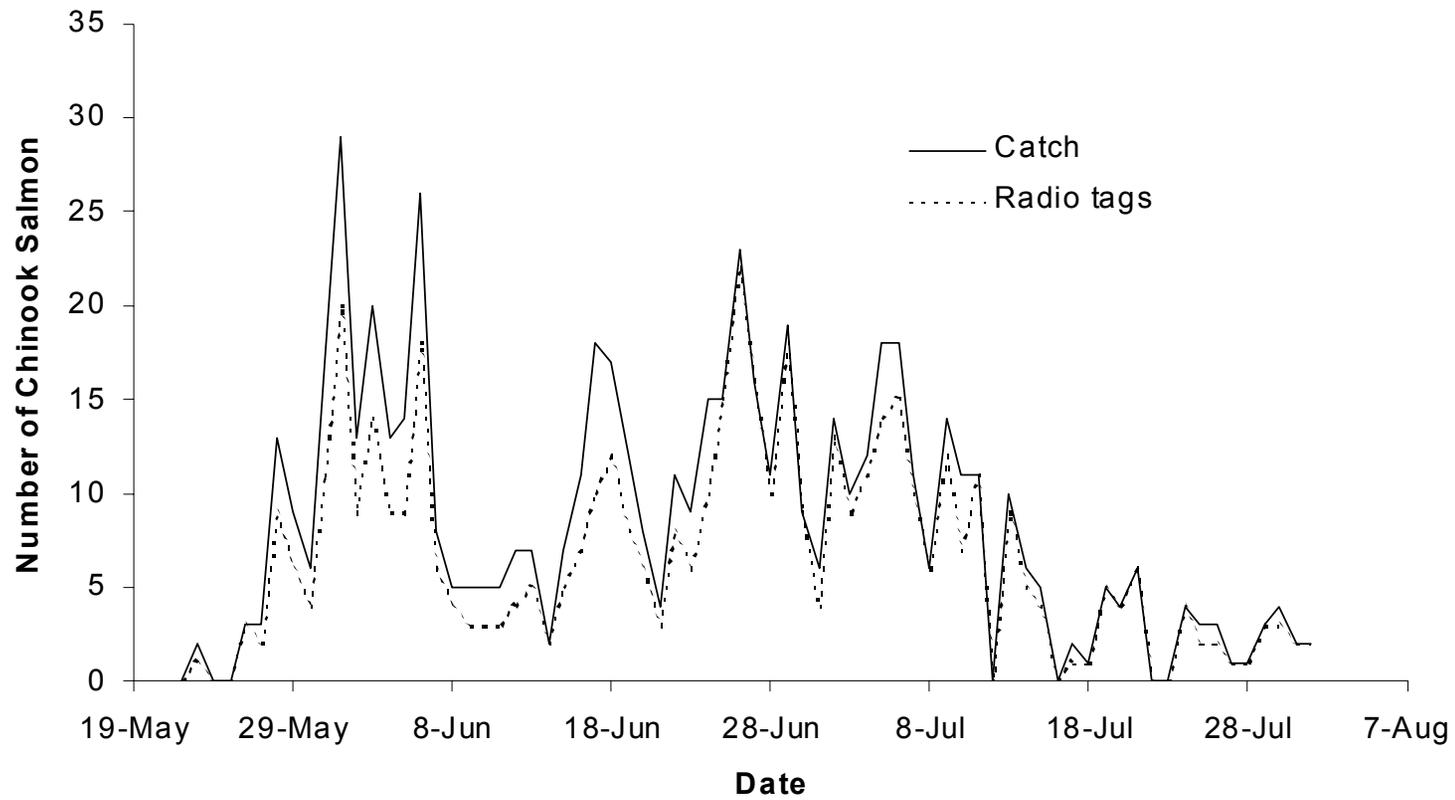


Figure 3.-Number of radio tags deployed each day and total daily catch of chinook salmon in the Copper River, 2001.

**Table 2.-Fates of radio-tagged chinook salmon in the Copper River, 2001.**

Fate <sup>a</sup>	Number of Tags
Total Deployed	480
Radio Failure	43
Total Entering CSS Fishery	437
CSS Fishery Recapture	35
Upriver Test Fishery Recapture	1
Total Fish Passing Through CSS fishery	377
Upstream Migrant <sup>b</sup>	83
Fish Wheel Recapture	9
Subsistence Fishery Mortality	16
Spawner	293
Sport Fishery Mortality	10

<sup>a</sup> Refer to Table 1 for definition of fates.

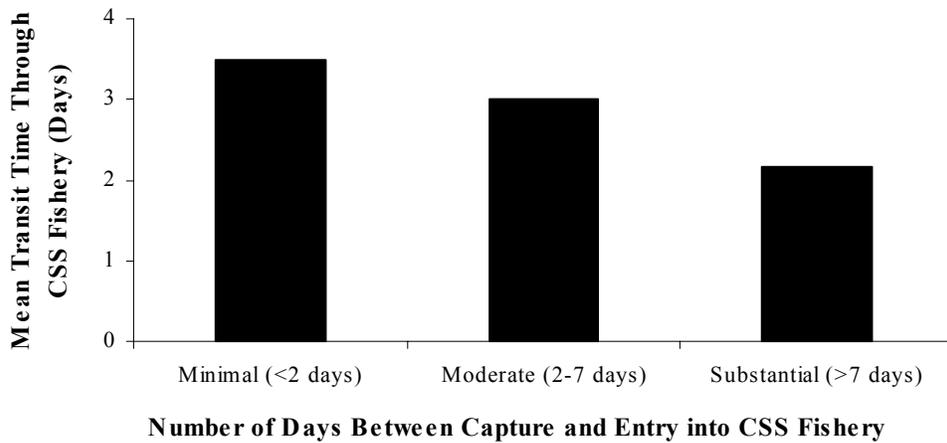
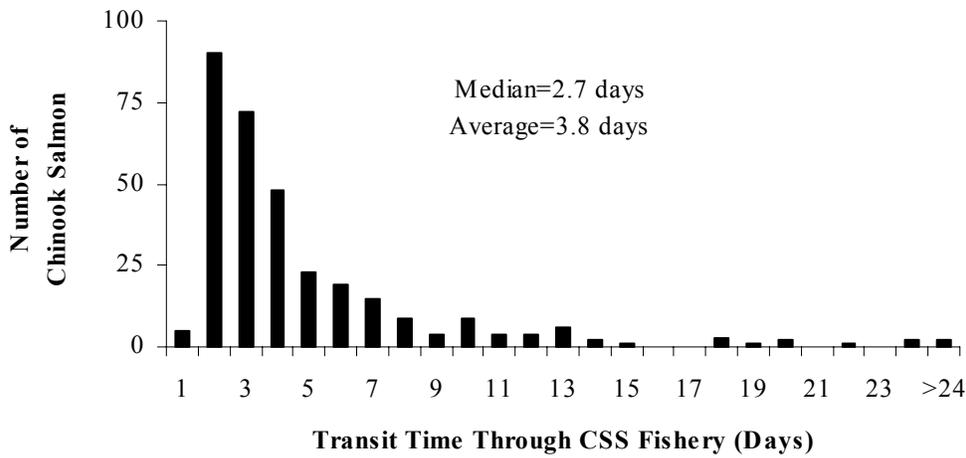
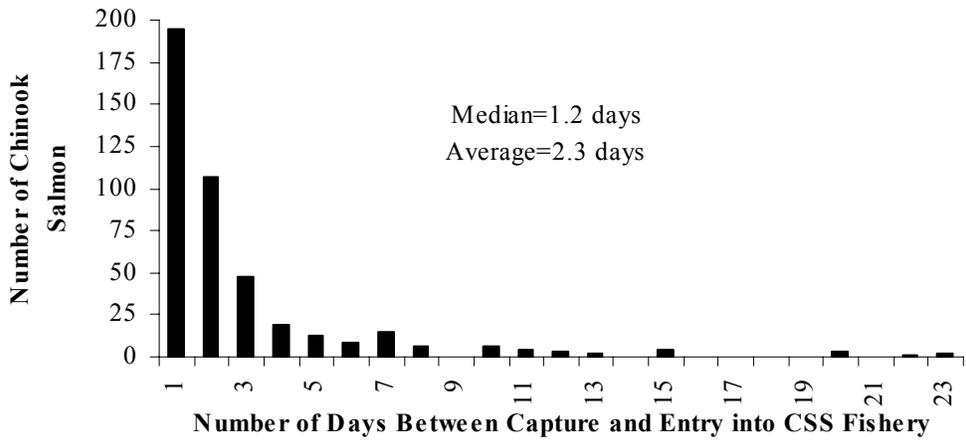
<sup>b</sup> Includes 24 tags that were recorded migrating upstream of the CSS fishery and never located again, 21 tags that passed through the CSS fishery and drifted back downstream, and 35 fish that were found in the mainstem of the Copper River upstream of the CSS fishery.

**Table 3.-Efficiency of tracking stations in detecting passing radio-tagged chinook salmon in the Copper River drainage, 2001.**

Station	Total tags known to pass site <sup>a</sup>	Number located during aerial surveys	Number logged by tracking station	Aerial tracking efficiency <sup>b</sup>	Station efficiency
Chitina R.	42	42	28	100.0%	66.7%
Klutina R.	84	65	84	77.4%	100.0%
Gulkana R.	48	43	40	89.6%	83.3%
Tonsina R.	68	65	67	95.6%	98.5%
Upper Copper R.	39	37	39	94.9%	100.0%
Copper R.	356		355		99.7%
O'brien Cr.	377		342		90.7%
Upper Haley Cr.	416		366		88.0%
Lower Haley Cr.	416		400		96.2%
Upper and Lower Haley Cr. Combined	437		437		100.0%

<sup>a</sup> Includes all fish logged by stations, located from aerial and boat surveys, and captured in the fisheries.

<sup>b</sup> Efficiency of aerial tracking was only evaluated for the spawning tributaries.



**Figure 4.-Delay after handling (top panel), transit times through the CSS fishery (middle panel), and a comparison of mean transit times through the CSS fishery of fish that exhibited minimal, moderate, and substantial delays (bottom panel) for radio-tagged chinook salmon in the Copper River, 2001.**

**Table 4.-Recapture rates for chinook salmon exhibiting minimal (<2 d), moderate (2-7 d), and substantial (>7 d) delays after handling, 2001.**

	Delay After Handling			Total
	< 2 days	2-7 days	> 7 days	
Recaptured	<b>34</b>	<b>9</b>	<b>5</b>	48
Not Recaptured	<b>269</b>	<b>100</b>	<b>20</b>	389
Total	303	109	25	437
Recapture Rate <sup>a</sup>	0.11	0.08	0.20	0.11

<sup>a</sup> Chi-square test for heterogeneity in recapture rates was performed for cells with bold numbers ( $\chi^2=2.92$ ; df=2; P=0.23).

CSS fishery. The remaining 437 radio-tagged fish either successfully migrated through, or harvested in the CSS fishery.

Movements between banks of tagged fish indicated that marked fish mixed with unmarked fish between sampling events. Of the 233 fish marked on the west bank that migrated into the CSS fishery, 10 were recaptured on the west bank and three were recaptured on the east bank (Table 5). Of the 247 fish marked on the east bank that migrated into the CSS fishery, seven were recaptured on the west bank and 11 were recaptured on the east bank. Based on radio tags returned with bank-of-capture information, marked chinook salmon exhibited similar recapture rates (Table 6;  $\chi^2=0.64$ ;  $df=1$ ,  $P=0.42$ ) and moved equally between banks (Table 7;  $\chi^2=5.02$ ;  $df=2$ ,  $P=0.08$ ).

The migration of radio-tagged chinook salmon not recaptured provided further evidence of mixing between banks. At the upper boundary of the CSS fishery, fish must migrate east to the Chitina River or continue west up the Copper River. Sixty percent of radio-tagged fish located in the Chitina River drainage were tagged on the west bank and crossed over to the east bank to complete their migrations. Similarly, 50% of fish that migrated to the west up the Copper River were tagged on the east bank.

The probability of a chinook salmon being recaptured was not influenced by its gender. Recapture rates of males (0.10) and females (0.12) were not significantly different ( $\chi^2=0.42$ ;  $df=2$ ;  $P=0.52$ ).

Size-selective sampling was detected for the first sample. Cumulative length frequency distributions of fish marked during the first event and fish recaptured during the second event (Test A) were not significantly different ( $DN=0.14$ ;  $P=0.33$ ; Figure 5). In contrast, cumulative length frequency distributions of marked fish during the first event and sampled fish during the second event (Test B) were significantly different ( $DN=0.16$ ;  $P<0.01$ ; Figure 5). Results of these tests indicated that an unstratified estimate of abundance was appropriate, but that only length, age, and sex data from the second sample be used to estimate composition proportions.

The probability of a chinook salmon being marked was independent of time of capture, and marked fish had equal probabilities of recapture despite their entry time into the CSS fishery (Table 8). Weekly marked to unmarked ratios were not significantly different ( $\chi^2=3.18$ ;  $df=8$ ;  $P=0.92$ ) and even though weekly recapture rates varied from 0.0-0.23 they were also not significantly different ( $\chi^2=9.72$ ;  $df=8$ ;  $P=0.29$ ).

Age composition of chinook salmon from the first and second samples were not statistically different ( $\chi^2=4.63$ ;  $df=6$ ;  $P=0.59$ ; Table 9). The largest proportion of the sample was age 1.3 (brood year 1996), as was the case in the previous two years of the study.

## **ABUNDANCE ESTIMATE**

Chapman's modified Petersen two-sample model (Seber 1982) was used to estimate inriver abundance of chinook salmon because the tests of consistency indicated that the model assumptions were met. An estimated 31,397 (SE = 4,280) chinook salmon  $\geq 620$  mm MEF entered the CSS fishery between 4 June and 6 August. The estimate was expanded using CPUE information from the first sample to account for fish that passed through the fishery prior to 4 June (Figure 6). The estimated proportion of the total run that migrated through the fishery from 4 June to 6 August was 0.79 (SE=0.15, Figure 7). Therefore, total estimated abundance

**Table 5.-Capture summaries for chinook salmon released on the east and west banks of the Copper River, 2001.**

Capture History	Released West Bank	Released East Bank	Total
Total Marked	233	247	480
Malfunctions	18	25	43
Number Entering CSS Fishery	215	222	437
Recaptured West Bank	10	7	17
Recaptured East Bank	3	11	14
Recaptured, but not Known Where	8	9	17
Total Recaptured	21	27	48
Number Not Recaptured	194	195	389
Recapture Rate	0.10	0.12	0.11

**Table 6.-Number of chinook salmon recaptured and not recaptured by bank of release and  $\chi^2$  result of test comparing recapture rates for fish marked on the east and west banks, 2001.**

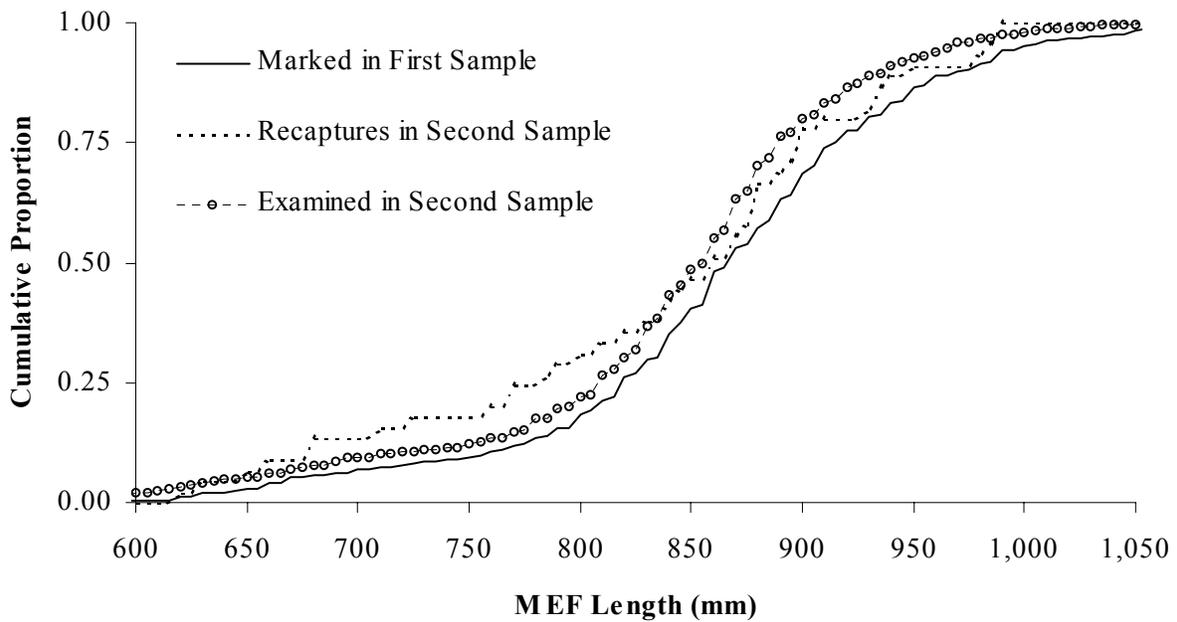
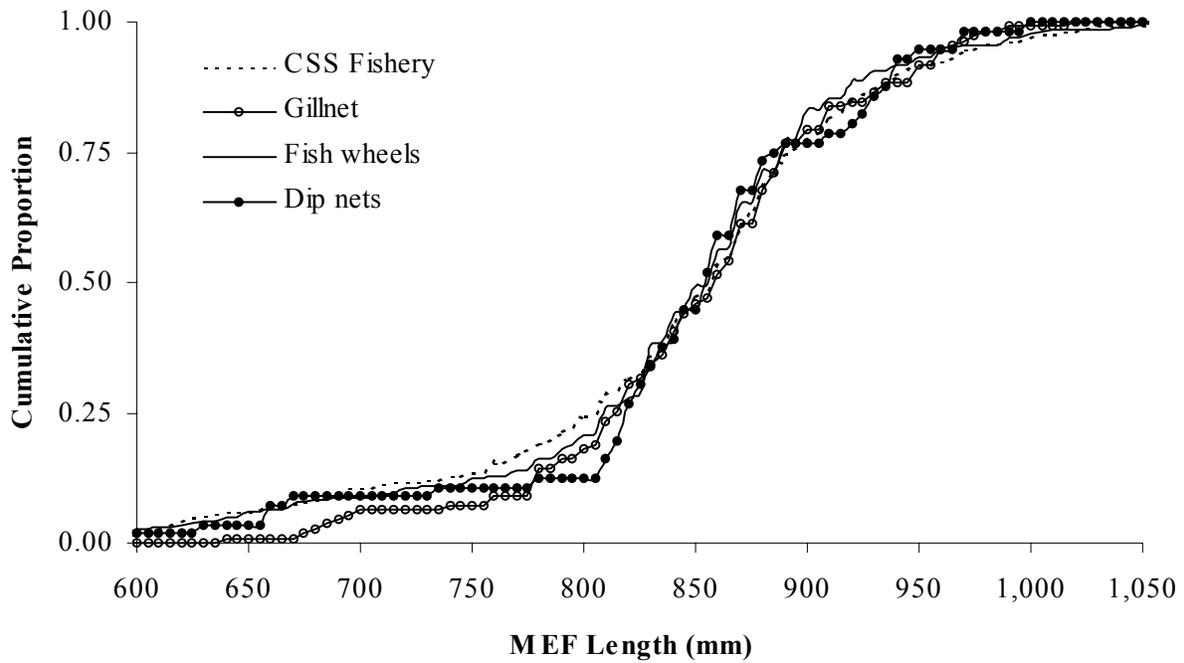
History of Recovery	Bank of Release	
	West	East
Recaptured	21	27
Not Recaptured	194	195

$\chi^2 = 0.64; df = 1; P = 0.42$

**Table 7.-Number of chinook salmon recaptured by bank of release and bank of recapture and  $\chi^2$  result of test comparing equal movement across the river, 2001.**

Bank of Recapture	Bank of Release	
	West	East
West	10	7
East	3	11
Not Recovered	194	195

$\chi^2=5.02; df=2; P=0.08$



**Figure 5.-Cumulative length frequency distributions of all fish examined during the second sample from the CSS fishery, gillnets, fish wheels, and dip nets (top panel), and all fish marked with radio tags during the first sample, all fish examined in the second sample, and all radio-tagged fish recaptured during the second sample (bottom panel), 2001.**

**Table 8.-Capture summaries for all chinook salmon marked and examined in the Copper River, 2001.**

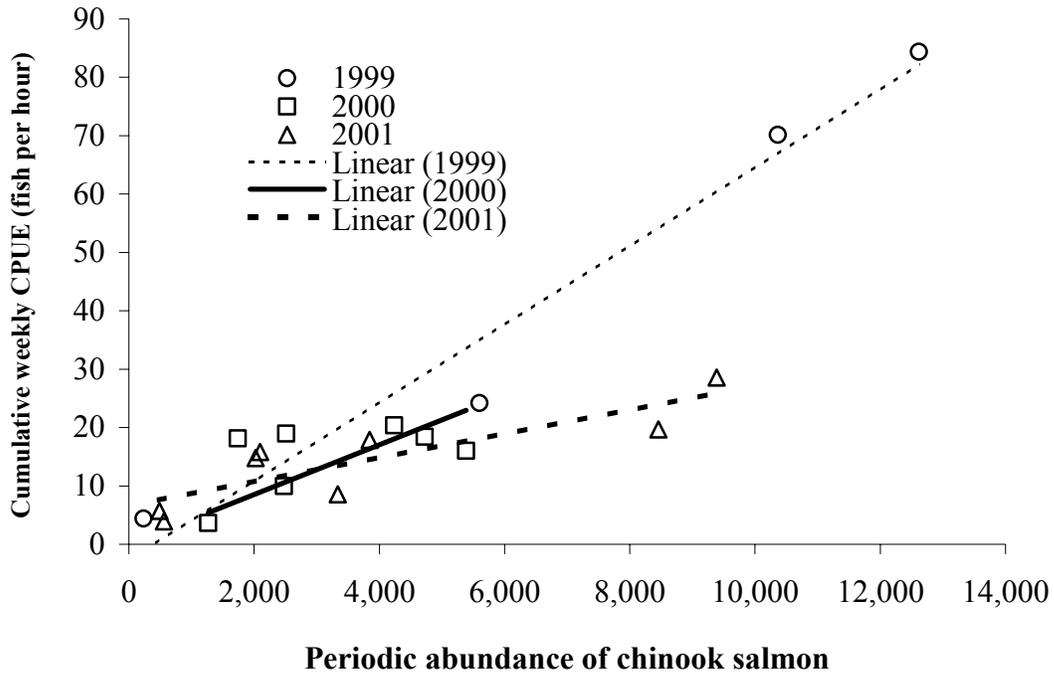
Week of Marking	Week of Recapture <sup>a</sup>									Number Recaptured	Number Marked	Number not Recaptured	Recapture Rate
	1	2	3	4	5	6	7	8	9				
0 (May 23-June 3)	0	0	0	0	0	0	0	0	0	0	40	40	0.00
1 (June 4-June 11)	7	1	0	0	0	0	0	0	0	8	84	76	0.10
2 (June 12-June 18)		5	1	0	0	0	0	0	0	6	26	20	0.23
3 (June 19-June 25)			2	5	0	0	0	0	0	7	39	32	0.18
4 (June 26-July 2)				6	0	1	0	0	0	7	93	86	0.08
5 (July 3-July 9)					8	0	0	0	0	8	80	72	0.10
6 (July 10-July 16)						5	1	0	0	6	46	40	0.13
7 (July 17-July 23)							2	0	0	2	7	5	0.29
8 (July 24-July 30)								1	0	1	14	13	0.07
9 (July 31-August 6)									0	0	8	8	0.00
Total Recaptured	7	6	3	11	8	6	3	1	0	45	437	392	0.11
Number Unmarked in Second Event	672	518	389	687	451	544	200	92	30				
Total Number fish Fish Examined	679	521	392	698	459	550	203	93	30				
Marked:Unmarked	0.010	0.012	0.008	0.016	0.018	0.011	0.015	0.011	0.000				

<sup>a</sup> Week of recapture was the same as week of marking. Weeks ran from Tuesday-Monday.

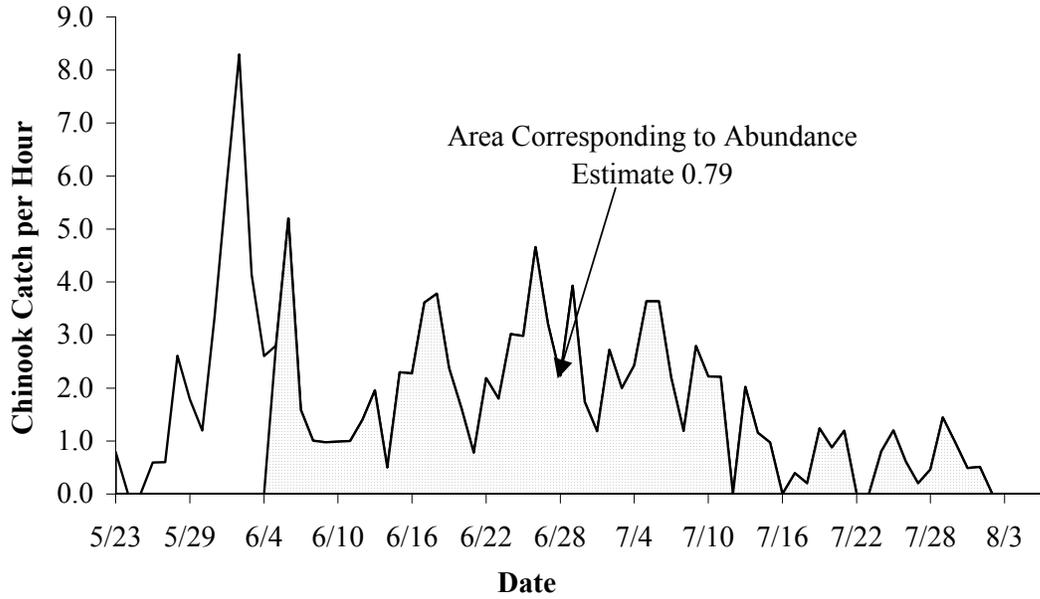
**Table 9.-Numbers of chinook salmon captured in the first sample and in subsistence fisheries (CSS fishery and GSS fishery combined) by age and brood year and contingency table analysis comparing age composition from the two samples, 2001.**

Age <sup>a</sup>	1.1	1.2	1.3	1.4	2.3	1.5	2.4
Brood Year	1998	1997	1996	1995	1995	1994	1994
First Sample	0	34	299	69	2	0	0
Subsistence fishery	4	80	639	133	8	1	2
Test Result $\chi^2= 4.63$ ; df=6; P=0.59							

<sup>a</sup> The notation x.x represents the number of scale annuli formed during river residence and ocean residence (i.e. an age of 1.3 represents one scale annuli formed during river residence and three scale annuli formed during ocean residence).



**Figure 6.-Periodic estimates of abundance of chinook salmon and cumulative periodic CPUE for 1999, 2000, and 2001. Periodic refers to a single week or pooled weeks.**



**Figure 7.-Catch per unit effort of chinook salmon during the first sample of the mark-recapture experiment and the proportion of the total CPUE (shaded) corresponding to the period of the abundance estimate in the Copper River, 2001.**

entering the CSS fishery from 22 May to 6 August was 39,778 (SE = 8,262) chinook salmon  $\geq$  620 mm MEF.

### **SPAWNING DISTRIBUTION**

Radio-tagged chinook salmon were located in all six major drainages of the Copper River (Table 10) including 34 tributary streams (Table 11). The smallest proportion returned to the Tazlina River (0.05) and the largest proportion returned to the Klutina River (0.26) (Figure 8). The proportion of chinook salmon detected in the nine aerial index streams accounted for 0.37 of chinook salmon in all spawning tributaries. Of the nine index streams, the Gulkana River accounted for the largest proportion of the total (Table 12).

No spawning activity was detected in the mainstem Copper River. Aerial surveys located 65 radio-tagged chinook salmon in the mainstem Copper River and boat surveys confirmed 23 of these as mortalities. The remaining radio-tagged fish exhibited no spawning behavior and either continued their upstream migrations or could not be located again. A majority of the radio-tagged chinook salmon in the Klutina and Tonsina rivers were located in the mainstem reaches of the rivers. It was assumed that chinook salmon were spawning in these areas as well as in the clearwater tributaries. Mainstem spawners accounted for 0.54 of all spawning chinook salmon in the Klutina River and 0.84 of those in the Tonsina River, which combined accounted for 0.35 of all spawning chinook salmon in the Copper River drainage (Table 13).

### **MIGRATORY TIMING**

Migratory time-density functions at the capture site of the entire run varied by year (Figure 9), and varied within 2001 among the individual spawning stocks (Figure 10). The mean date of passage for all chinook salmon captured in 2001 was 16 June and ranged from 2 June for the upper Copper River drainage to 5 July for the mainstem Klutina River (Table 14). The mean date of passage varied for all stocks in all three years of the study, but individual stocks displayed similar patterns between years (Figure 11). Migratory timing of chinook salmon bound for tributaries of the Tonsina and Klutina rivers was earlier than their mainstem spawning counterparts (Figure 12).

## **DISCUSSION**

This was the third and final year (1999-2001) of a study that estimated the abundance, spawning distribution, and migratory timing of chinook salmon in the Copper River drainage. In all three years a similar study design was used to estimate the abundance of chinook salmon at the point of entry into CSS fishery. Experimental assumptions such as tag loss, emigration, and mortality were explicitly tested because the fates of all radio-tagged fish were known. Even though the consistency tests indicated the estimate of abundance was unbiased, potential bias from factors such as unreported harvest, illegal harvest, selection for tagged fish, inability to detect radio-tagged fish that were harvested, and removal of tags could not be explicitly tested.

Unreported or illegal harvest would negatively bias the estimate of chinook salmon abundance. Unreported harvest is defined as a permitted CSS fisher who harvested chinook salmon and did not return their permit, while illegal harvest is defined as fishers who harvested chinook salmon without a permit. The number of chinook salmon harvested by CSS fishers who did not return their permits was estimated based on harvest rate trends from CSS fishers that returned their permits after multiple reminder letters. The high return rate of permits (88%), coupled with

**Table 10.-Distribution of radio-tagged chinook salmon in major spawning drainages in the Copper River, 1999-2001.**

Spawning Stream	1999		2000		2001	
	Proportion of All Spawners <sup>a</sup>	Percentile Limits (2.5 <sup>th</sup> ,97.5 <sup>th</sup> )	Proportion of All Spawners <sup>a</sup>	Percentile Limits (2.5 <sup>th</sup> ,97.5 <sup>th</sup> )	Proportion of All Spawners <sup>a</sup>	Percentile Limits (2.5 <sup>th</sup> ,97.5 <sup>th</sup> )
Chitina River	0.22	(0.18, 0.27)	0.13	(0.09, 0.16)	0.14	(0.10, 0.19)
Gulkana River	0.12	(0.08, 0.16)	0.25	(0.21, 0.30)	0.18	(0.14, 0.24)
Klutina River	0.27	(0.22, 0.33)	0.27	(0.22, 0.32)	0.26	(0.21, 0.31)
Tazlina River	0.03	(0.02, 0.06)	0.03	(0.02, 0.06)	0.05	(0.02, 0.08)
Tonsina River	0.24	(0.20, 0.29)	0.20	(0.16, 0.25)	0.21	(0.17, 0.26)
Upper Copper River						
Tributaries	0.11	(0.08, 0.14)	0.12	(0.09, 0.15)	0.15	(0.11, 0.20)

<sup>a</sup> Adjusted for daily tagging rates and fishing effort.

**Table 11.-Numbers of radio-tagged chinook salmon located in tributaries of the Copper River during aerial tracking surveys, 1999-2001.**

Tributary	Number of Radio-tagged Chinook Salmon		
	1999	2000	2001
<b>Upper Copper River Drainage</b>			
Mainstem Copper River	0	6	4
Ahtell River	2	0	1
Bone Creek	1	3	4
Chistochina River (mainstem)	2	4	5
E. Fork Chistochina River	6	7	12
No Name (south of E. Fork Chistochina River)	2	1	0
Sinona Creek	2	2	1
Gakona River (mainstem)	4	0	4
Spring Creek	2	4	5
No Name (Opposite Spring Creek)	2	1	1
Indian River	2	3	3
Drop Creek	3	1	2
Tulsona Creek	0	0	1
No Name (east side parallel to Drop Creek)	0	1	1
No Name (east side opposite Indian River)	2	2	1
No Name (east side opposite Sinona Creek)	1	1	0
No Name (east side upstream of Yokneda Lakes)	1	1	1
<b>Gulkana River Drainage</b>			
Gulkana River (mainstem)	14	58	29
Middle Fork Gulkana River	3	1	5
West Fork Gulkana River	3	1	5
Hungry Hollow Creek	1	0	1
Paxson Lake Outlet	1	3	1
No Name (west side upstream of West Fork)	0	3	0

-continued-

**Table 11.-Page 2 of 2.**

<b>Tributary</b>	<b>Number of Radio Tagged Chinook Salmon</b>		
	<b>1999</b>	<b>2000</b>	<b>2001</b>
<b>Tazlina River Drainage</b>			
Kiana Creek	5	7	6
Mendeltna Creek	4	2	5
<b>Klutina River Drainage</b>			
Klutina River (mainstem)	46	58	57
Manker Creek	13	11	10
St. Anne Creek	3	5	8
Mahlo Creek	0	1	1
<b>Tonsina River Drainage</b>			
Tonsina River (mainstem)	51	45	56
Greyling Creek	8	8	4
Little Tonsina River	7	1	3
Dust Creek	1	1	1
Bernard Creek	1	0	0
<b>Chitina River Drainage</b>			
Chitina River (Mainstem)	0	5	0
Chakina River	12	8	6
Gilahina River	3	9	9
Lakina River	3	1	1
Monahan Creek	2	2	6
Tana River	6	1	2
Tebay River	35	11	18

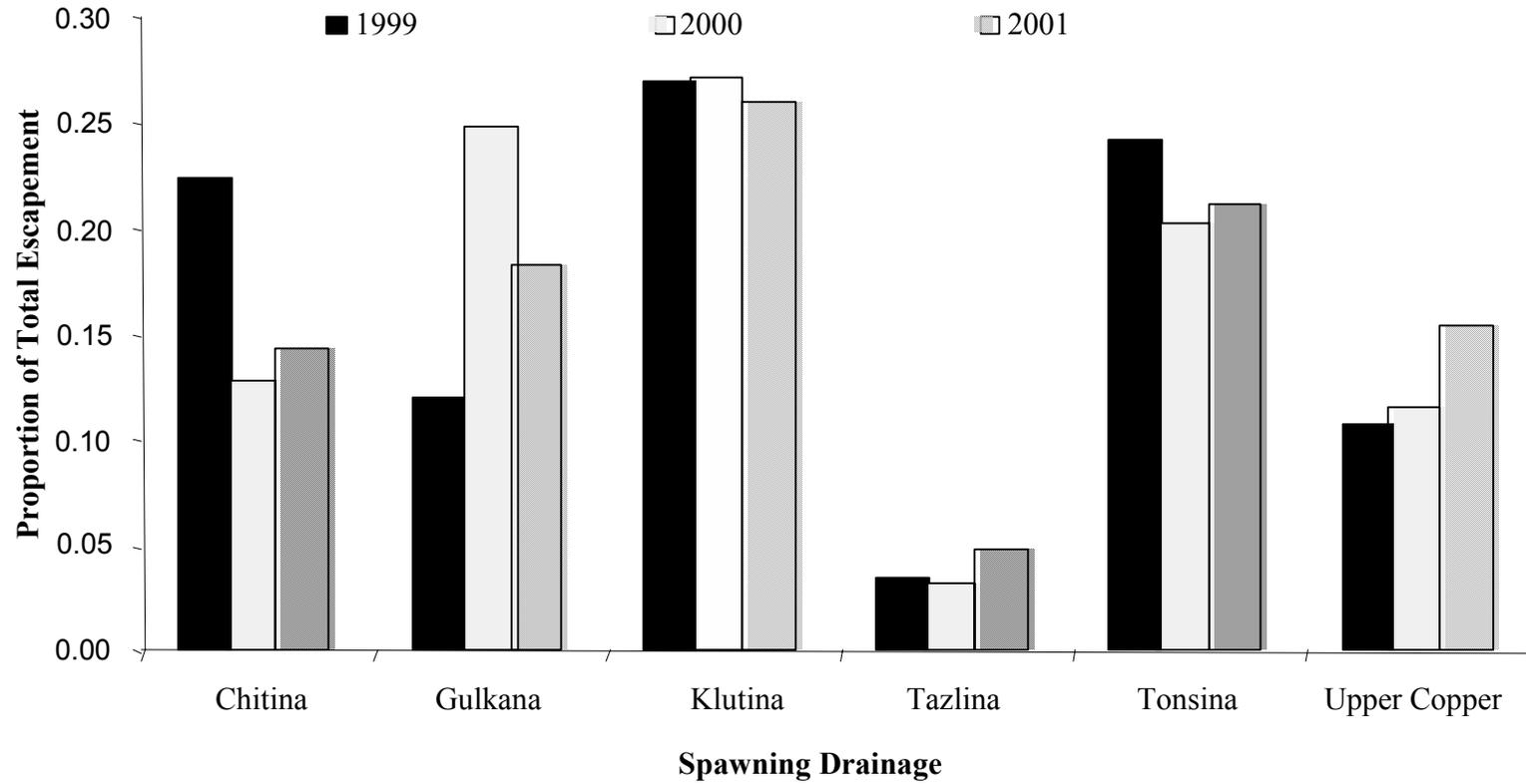


Figure 8.—Spawning distribution of Copper River chinook salmon by major drainage.

**Table 12.-Proportions of radio-tagged chinook salmon located in nine aerial survey index streams in the Copper River drainage, 1999-2001.**

Spawning Stream	1999		2000		2001	
	Proportion of All Spawners <sup>a</sup>	Percentile Limits (2.5 <sup>th</sup> ,97.5 <sup>th</sup> )	Proportion of All Spawners <sup>a</sup>	Percentile Limits (2.5 <sup>th</sup> ,97.5 <sup>th</sup> )	Proportion of All Spawners <sup>a</sup>	Percentile Limits (2.5 <sup>th</sup> ,97.5 <sup>th</sup> )
Gulkana River	0.12	(0.08, 0.16)	0.25	(0.20, 0.30)	0.18	(0.13, 0.24)
E. Fork Chistochina River	0.02	(0.01, 0.04)	0.02	(0.01, 0.04)	0.05	(0.02, 0.08)
Manker Creek	0.04	(0.02, 0.06)	0.04	(0.02, 0.07)	0.03	(0.01, 0.06)
St. Anne Creek	0.01	(0.00, 0.02)	0.02	(0.00, 0.03)	0.03	(0.01, 0.04)
Little Tonsina River	0.02	(0.01, 0.04)	<0.01	(0.00, 0.01)	0.01	(0.00, 0.02)
Greyling Creek	0.02	(0.01, 0.04)	0.02	(0.01, 0.04)	0.01	(0.00, 0.03)
Indian Creek	<0.01	(0.00, 0.01)	0.01	(0.00, 0.02)	0.01	(0.00, 0.02)
Kiana Creek	0.01	(0.01, 0.03)	0.03	(0.01, 0.05)	0.02	(0.01, 0.04)
Mendeltna Creek	0.01	(0.00, 0.02)	0.01	(0.00, 0.02)	0.02	(0.00, 0.05)
Proportion of Total in Index Streams	0.26	(0.21, 0.31)	0.40	(0.34, 0.45)	0.37	(0.30, 0.43)

<sup>a</sup> Adjusted for daily tagging rates and fishing effort.

**Table 13.-Proportions of chinook salmon spawning in the mainstem and tributaries of the Tonsina and Klutina rivers, 2001.**

River	Number of Radio Tags	Proportion of Spawners <sup>a</sup>	Percentile Limits (2.5 <sup>th</sup> , 97.5 <sup>th</sup> )
Tonsina River			
Mainstem	60	0.87	(0.67,1.00)
Greyling Creek	4	0.07	(0.02,0.14)
L. Tonsina River	3	0.05	(0.00,0.11)
Bernard Creek	0	0.00	(0.00,0.00)
Dust Creek	1	0.01	(0.00,0.04)
All Tributaries	8	0.13	(0.05,0.21)
Klutina River			
Mainstem	65	0.76	(0.58,0.93)
Manker Creek	10	0.13	(0.05,0.21)
St. Anne Creek	8	0.10	(0.04,0.17)
Mahlo Creek	1	0.01	(0.00,0.04)
All Tributaries	19	0.24	(0.14,0.35)

<sup>a</sup> Adjusted for daily tagging rates and fishing effort.

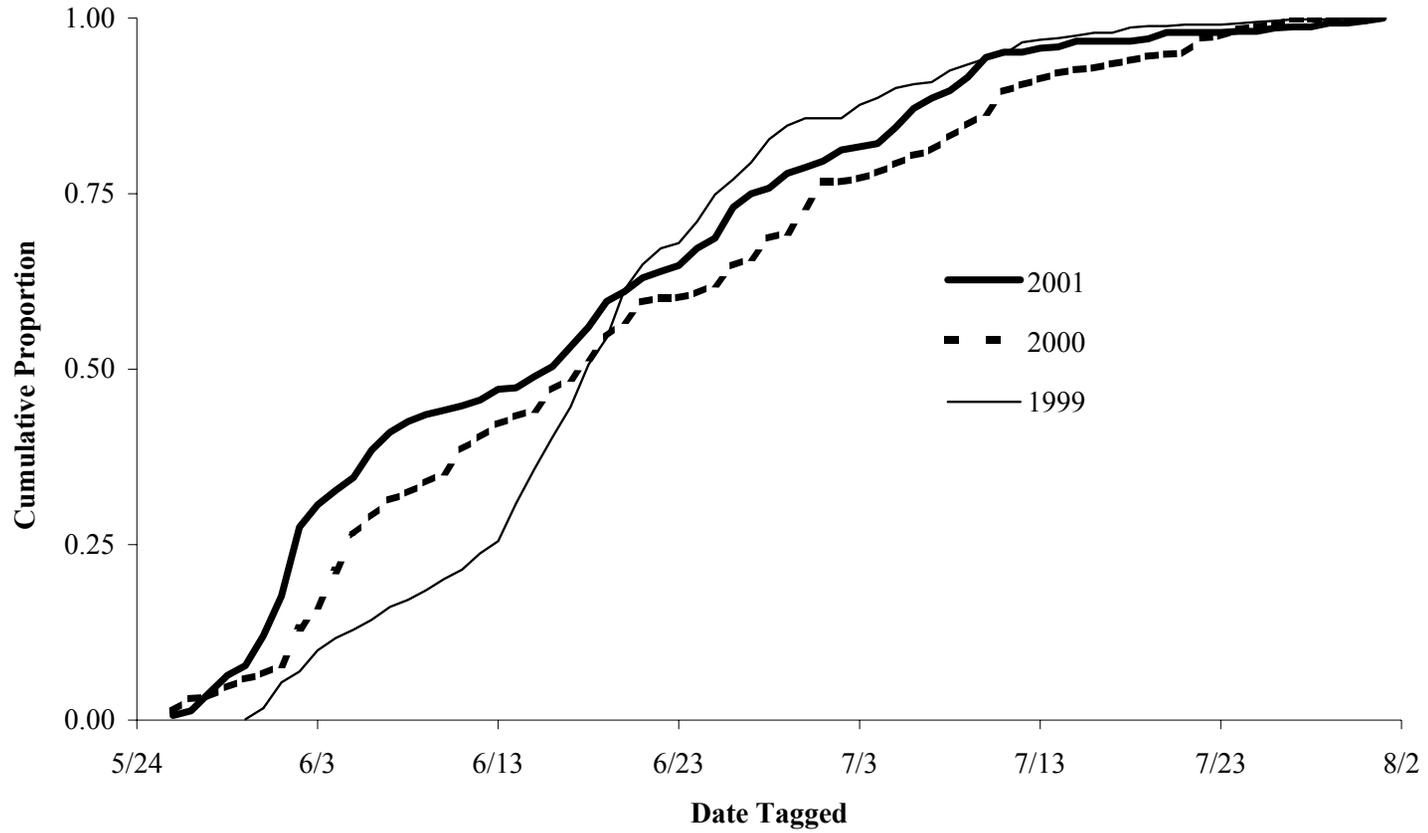


Figure 9.-Migratory-timing profiles for the entire run of chinook salmon at the capture site in the Copper River drainage, 1999-2001.

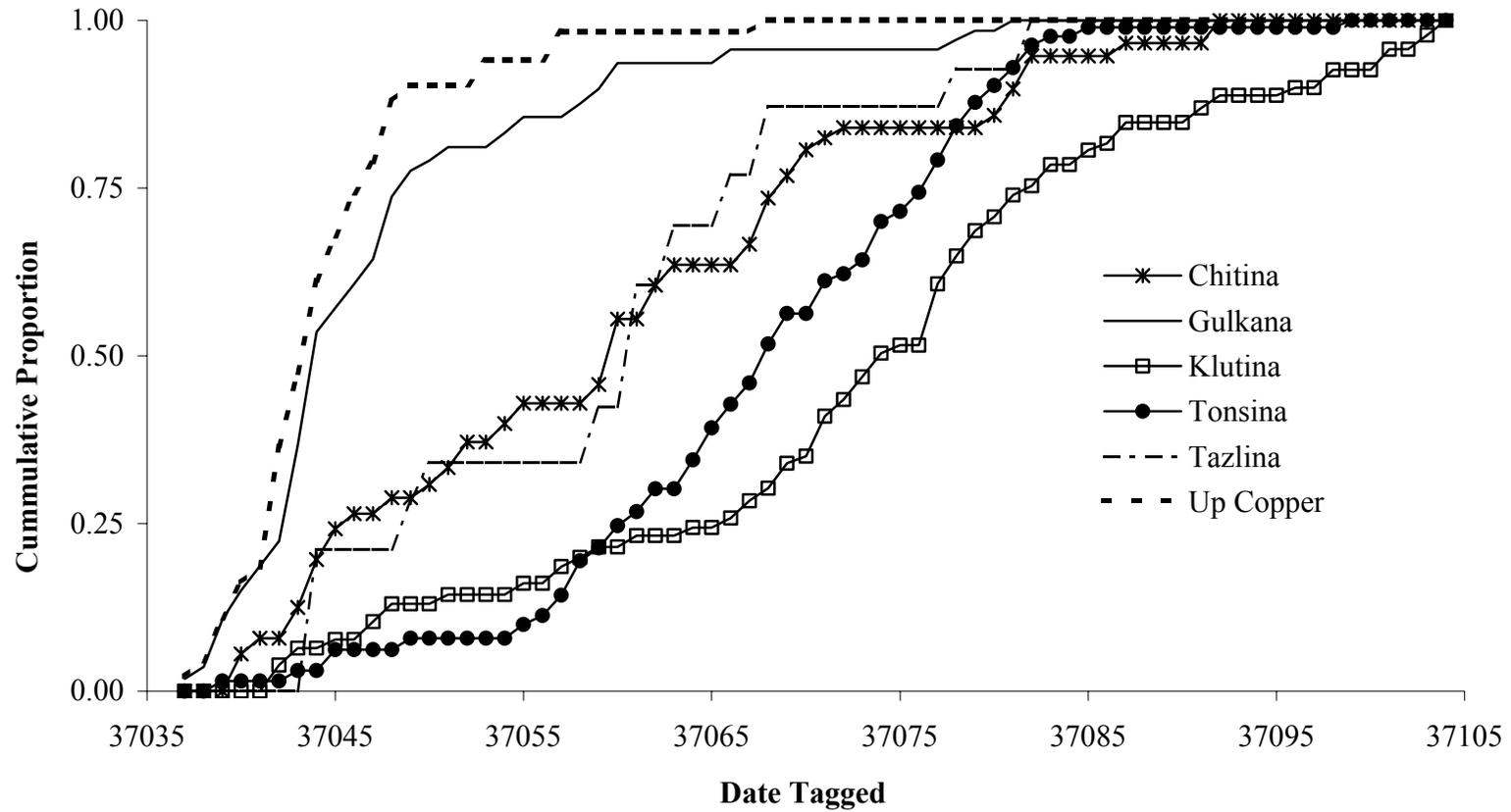


Figure 10.-Migratory-timing profiles of chinook salmon at the capture site for the major stocks in the Copper River drainage, 2001.

**Table 14.-Statistics regarding the migratory timing past the capture site of the major chinook salmon spawning stocks in the Copper River, 2001.**

Spawning Stock	Duration (No. of Days)	Mean Date of Passage ( $\bar{t}$ )	SE ( $\bar{t}$ )
Upper Copper River	5/26-6/26 (31)	6/2	5.2
Gulkana River	5/26-7/9 (44)	6/5	9.2
Chitina River	5/29-7/20 (52)	6/18	14.3
Tazlina River	6/2-7/10 (38)	6/17	11.5
Tonsina River (All)	5/28-7/27 (60)	6/25	10.8
Mainstem	5/28-7/27 (60)	6/25	9.9
Tributaries	6/3-7/2 (29)	6/15	11.6
Klutina River (All)	5/31-8/1 (62)	7/1	16.1
Mainstem	6/3-8/1 (59)	7/5	13.3
Tributaries	5/31-7/15 (45)	6/12	12.4

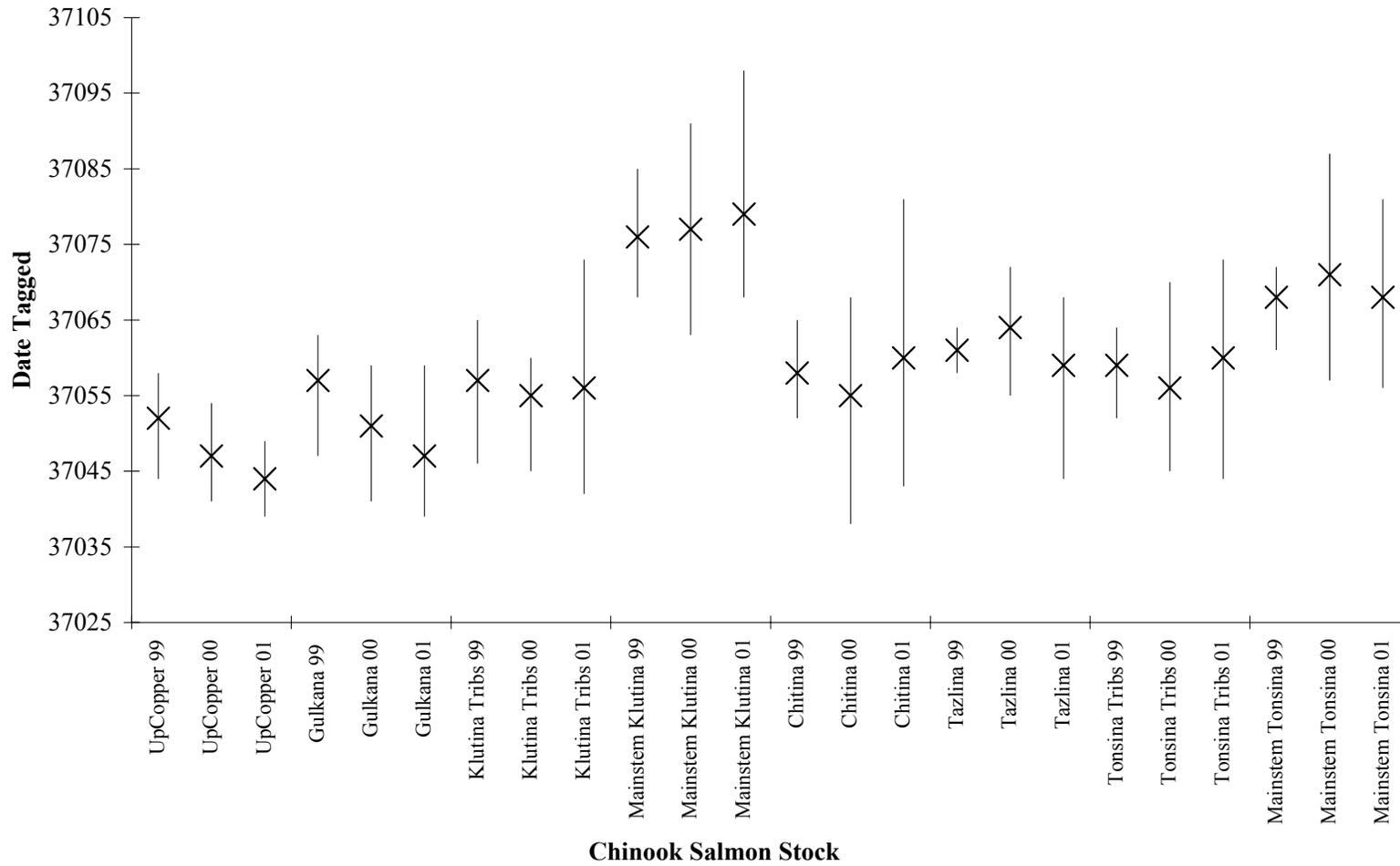
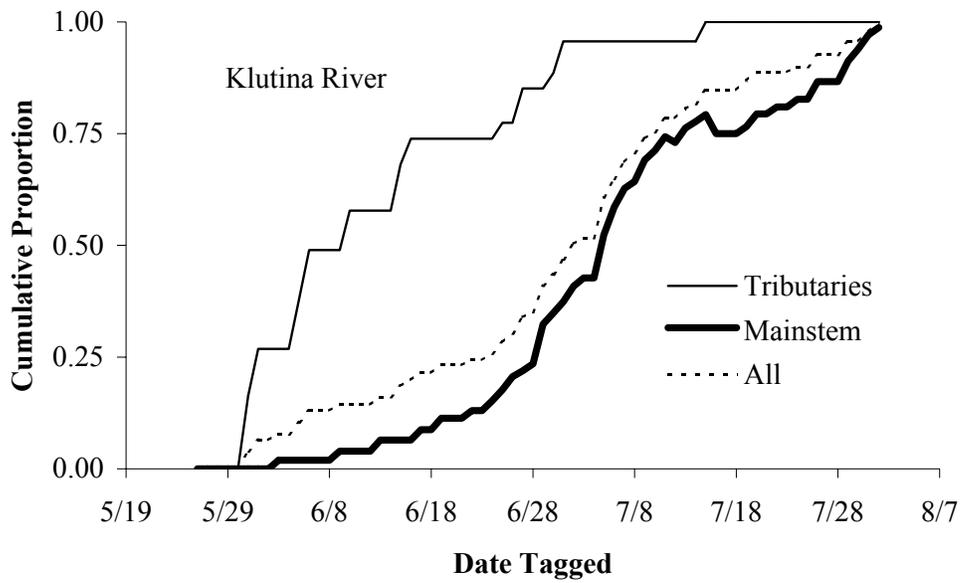
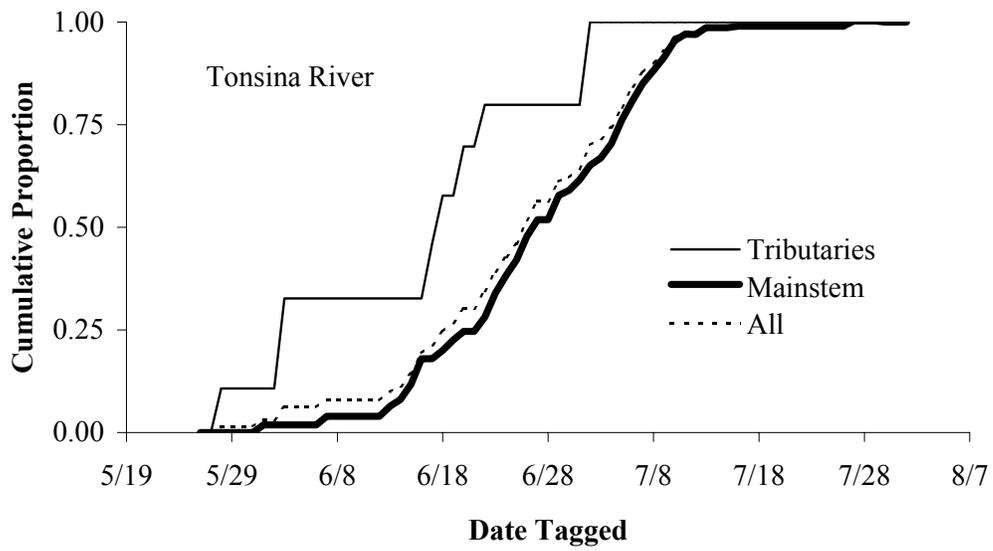


Figure 11.-Mean passage date (symbol) and 80% range (vertical lines) of Copper River chinook salmon stocks at the capture site in 1999-2001.



**Figure 12.-Migratory-timing profiles of chinook salmon in the Tonsina and Klutina rivers for tributary and mainstem spawners, 2001.**

observations that persons who did not return permits tended to harvest fewer fish than persons who did return permits suggested that the unreported harvest was negligible. Illegally harvested chinook salmon would only have biased the estimate if the harvested fish were tagged. Tagged fish were used in the estimation whether they were reported or not, whereas unmarked fish not reported were not. Thirty of the 35 radio-tagged fish harvested in the CSS fishery were returned by fishers holding a permit. The remaining five were harvested when the fishery was open, but it is not known whether they were harvested by permit holders.

Failure to detect radio-tagged chinook salmon harvested in the CSS fishery would have biased the estimate of chinook salmon abundance high. The probability that this situation occurred was low because tracking stations located at the upper and lower boundaries of the CSS fishery and O'Brien Creek were able to detect all radio-tagged fish that entered and exited the fishery. Nearly all radios from tagged fish captured by CSS fishers (30 of 35) were voluntarily returned. Five tags were assumed harvested based on large signal strength recordings at O'Brien Creek and/or Haley Creek tracking stations.

Selection for radio-tagged chinook salmon by CSS fishers would have negatively biased the estimate of abundance. Although there were likely many CSS fishers who caught more than one chinook salmon, it is unlikely that they retained or released fish because the fish were tagged. There was no reward offered for returned tags. In addition, gray-colored spaghetti tags were used and were difficult to immediately detect. Several CSS fishers stated they did not notice the spaghetti or radio tag until they had processed their fish.

Removal and return of radio tags from chinook salmon that were not harvested would negatively bias the abundance estimate. When possible, fishers who returned tags were asked whether the tagged fish was harvested or released. None of the CSS fishers that were queried indicated that they had removed a tag and released a fish.

The design of the mark-recapture experiment incorporated the harvest of chinook salmon in the CSS fishery for the second sample. The advantages of this were that a large number of fish were examined for marks, the additional cost to the experiment was minimal, and relatively few fish needed to be handled and marked. However, frequent and prolonged fishery openings were required to estimate chinook salmon abundance, especially in June when a large portion of the run was passing through the study area. Even with early fishery openings (by statute the fishery cannot open before 1 June), a portion of the early run had already migrated through the study area. In 2001, the CSS fishery opened on 4 June and there were few closures thereafter. This allowed us to use the harvest to estimate abundance for 79% of the run. Prior to the opening of the fishery on 4 June, marked fish from the first sample were passing through the area of the fishery, but their probability of capture was zero. Therefore, to estimate abundance for this period, we expanded the mark-recapture estimate of abundance for the period during the fishery by the proportion of the total run it represented. We then utilized the relationship between periodic estimates of CPUE in the marking event and their corresponding estimate of abundance for periods when the fishery was open and applied this relationship to the estimate of abundance when the fishery was closed to model uncertainty in the estimate. The estimated proportion of the run accounted for by the mark-recapture study incorporated two sources of uncertainty because the variation in the relationship between cumulative weekly CPUE (process error) and weekly abundance estimates (measurement error) is characteristic of the uncertainty in estimating total abundance (Figure 6). The variation associated with this method of estimation was greater than the variation associated observed with the mark-recapture model. Thus, active

sampling in late May and early June to incorporate into the mark-recapture model is preferred to the expansion technique. Future studies should incorporate sampling of subsistence fish wheel catches near the McCarthy Road Bridge. There are numerous fish wheels that operate in this area and catches are generally high early in the season. Federally-qualified users can begin fishing on 15 May.

During the 2000 season the fishery was not opened on a continuous basis until June 16, which prevented obtaining a sample during early June when a large portion of the run was passing. Therefore, during the 2001 season, additional sampling in the area of the fishery was added to the design to ensure that fish were examined in the second sample during June. In 2001, subsistence fishers in the Glennallen subdistrict could begin fishing on 1 June. Sampling of subsistence fishers upstream of the McCarthy Road Bridge was productive and catches averaged 8.3 and ranged from 1-37 chinook salmon per day. Gillnetting chinook salmon was also useful. Catches averaged 11.2 and ranged from 5-21 fish per day. A comparison of the cumulative length distributions detected no significant difference between fish sampled from subsistence dip nets, fish wheels, and gillnets.

The affects of inserting radio tags into chinook salmon are not fully understood. The proportion of radio-tagged chinook salmon that failed to migrate upstream varied between 4% (n=14) in 1999, 10% (n=56) in 2000, and 9% (n=43) in 2001. Comparable studies on chinook salmon in the Stikine and Taku rivers in Southeast Alaska have observed similar failure or retreat rates (Pahlke and Bernard 1996; Bernard et al. 1999). Even though the failure rates observed in this study are not uncommon, the central question of whether handling affects the probability of capture in the second sample still remains. One measure of this handling affect was the delay in migration after the fish has been tagged. The assumption was that any delay in their migration was a relative measure of stress, and stressed fish may have migrated upstream in nearshore waters with lower velocities. In this situation a radio-tagged chinook salmon would have been more vulnerable to capture by shore-positioned dipnetters. Similar recapture rates between fish that exhibited minimal, moderate, and substantial delays coupled with comparable transit times through the CSS fishery suggested that any handling-induced changes did not affect the probability of capture.

The ground-based investigations conducted in 2001 to determine the spawning status of radio tags located in the mainstem Copper River revealed no evidence of spawning activity. Studies have shown that chinook salmon are capable of spawning in mainstem, glacial rivers, but these systems are typically buffered by large lakes that reduce turbidity and extreme summer flows (Burger et al. 1985; Evenson and Wuttig 2000). Due to high water, a number of radio tags could not be recovered. However, all of the radio tags located were in areas of deep, fast water with silt-laden substrates or piles of debris located on the sandbars. One radio tag was recovered from an area associated with bear feeding activity. Wuttig and Evenson (2001) recovered a radio tag from a chinook salmon carcass adjacent to another chinook salmon that had neither spawned nor been tagged, which implies that some tagged fish may have died from natural causes. The fact that no radio tags were located in an area indicative of chinook salmon spawning suggests that radio tags located in the mainstem Copper River were either expelled and/or were associated with a fish that died prior to spawning.

Monan and Liscom (1975) believe that spring and fall run chinook salmon can successfully migrate to their spawning grounds when fitted with internal radio tags. In contrast, Gray and Haynes (1979) found that the proportion of chinook salmon fitted with internal radio tags that

returned to their spawning grounds was significantly less than fish tagged with only spaghetti tags. They concluded that the majority of unsuccessful migrations were caused by placing the radio tag well into the stomach instead of just behind the esophageal sphincter or anterior stomach. This study placed radio tags in the anterior stomach of chinook salmon and 78% of the tagged fish that migrated through the CSS fishery were located in a spawning tributary. These results imply that correctly placed internal radio tags will not influence the migration of spawning chinook salmon.

The spawning distribution of chinook salmon in the Copper River drainage from 1999-2001 indicated the nine spawning streams that are aerial surveyed annually for an index of escapement represented a small and variable proportion of the total drainage-wide escapement. Chinook salmon located in the nine index streams only accounted for 26% (1999), 40% (2000), and 37% (2001) of all spawning fish. The largest contributor to the total escapement count was the Gulkana River that accounted for 47% of the escapement in the index streams in 1999 and 63% in 2000 and 2001. However, escapement in the Gulkana River represented only 12%, 25%, and 18%, respectively, of the total drainage-wide escapement. Management decisions based on these aerial counts are subject to a substantial amount of uncertainty and efforts should be taken to improve enumeration techniques and determine whether these are the most appropriate streams to provide an index of escapement.

In 1999-2001 the run timing of chinook salmon at the capture site revealed that upriver stocks, such as the Gulkana River stock, were the first to enter the CSS fishery and downriver stocks, such as the Klutina River stock, were the last. This type of run timing pattern where upriver stocks enter first inriver and downriver stocks enter last has been observed in other large salmon river systems (Koski et al. 1994; Pahlke and Bernard 1996). If this run timing holds true at the mouth of the Copper River, where fish are vulnerable to the commercial fishery, then it is probable that individual stocks are subject to varying levels of exploitation.

As in previous years of the study, the majority of radio tags located within the Klutina and Tonsina rivers were located in the mainstem portions of the rivers. In 1999, mainstem spawners in these two rivers represented 33% of all spawning chinook salmon. This number increased to 40% in 2000 and then dropped slightly to 39% in 2001. This is the largest component of the spawning population and it has never been assessed because both rivers are large, fast-flowing, and glacially occluded, which makes aerial surveys and other assessment techniques difficult to perform. Continued radiotelemetry studies may be the only effective means of assessing escapements in these systems.

Another characteristic shared by the chinook salmon stocks in the Tonsina and Klutina rivers is the run timing of the mainstem and tributary spawners. In all three years of the study, tributary spawners were the first to arrive inriver and mainstem spawners arrived a measurable time later (Figure 11). These behavioral differences are analogous to the early and late-run stocks of the Kenai River. Burger et al. (1985) suggested that Kenai and Skilak lakes increase the fall and winter temperatures of downstream waters in the Kenai River, enabling successful reproduction for late-run mainstem spawners. Both Klutina and Tonsina rivers have large lakes at their headwaters that may increase the temperature of mainstem waters, and may enable eggs to incubate faster than their tributary counterparts. In contrast, Beer and Anderson (2001) found that progeny from early-run tributary spawners in the Methow River, Washington exhibit a wide range of emergence times after absorption of the yolk sac, whereas late-run mainstem progeny synchronized emergent times below optimal mass with a visible yolk sac. Because natural

selection ensures that the timing of spawning will optimize fry survival, upstream fry may need a wide range of emergent times to maximize limited upstream habitat (Beer and Anderson 2001). Furthermore, downstream fry may emerge together to saturate predators (Brannas 1995) because predator avoidance is limited when the yolk sac is not completely absorbed (Thomas et al. 1969).

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