Fishery Data Series No. 12-57

Inriver Abundance and Spawner Distribution of Kenai River Sockeye Salmon *Oncorhynchus nerka*, 2006-2008: A Comparison of Sonar and Mark–Recapture Estimates

by

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October 2012

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

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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

FISHERY DATA SERIES NO. 12-57

INRIVER ABUNDANCE AND SPAWNER DISTRIBUTION OF KENAI RIVER SOCKEYE SALMON *ONCORHYNCHUS NERKA*, 2006-2008: A COMPARISON OF SONAR AND MARK–RECAPTURE ESTIMATES

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October 2012

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This document should be cited as:
Willette, T. M., T. McKinley, R. D. DeCino, and X. Zhang. 2012. Inriver abundance and spawner distribution of Kenai River sockeye salmon, Oncorhynchus nerka, 2006-2008: a comparison of sonar and mark–recapture estimates. Alaska Department of Fish and Game, Fishery Data Series No. 12-57, Anchorage.

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ABSTRACT

The escapement of sockeye salmon, *Oncorhynchus nerka*, into the Kenai River has been estimated using a combination of sonar and fish wheels operated at rkm 31.1 since 1968. Beginning in 2011, the fisheries were managed using a dual-frequency identification sonar (DIDSON). This project used mark–recapture methods to independently investigate bias in DIDSON estimates of sockeye salmon escapement in 2006–2008. Mark–recapture experiments were conducted using passive integrated transponder tags, radio tags, fish wheels, and weirs (Russian River and Hidden Creek) as recapture sites. Radiotelemetry was used primarily to identify spawning areas throughout the watershed and estimate tagging-induced mortality. Overall, our mark–recapture abundance estimates did not support the conclusion that the DIDSON estimates were consistently biased during the 3 years of this study. In 2006, the Russian mark–recapture estimate was significantly higher while the Hidden mark–recapture estimate was significantly lower than the DIDSON estimate. Variable tagging-induced mortality or initial capture probabilities between the 2 stocks were likely causes of these observed differences. In 2007, the mark–recapture estimates from both weirs were not different from the DIDSON estimate. However in 2008, the Russian mark–recapture estimate was not different while the Hidden mark–recapture estimate was significantly lower than the DIDSON estimate. A linear regression of the pooled mark–recapture estimates (dependent variable) against the DIDSON estimates (2006–2008) resulted in an intercept not significantly different from zero and a slope not significantly different from one. Radiotelemetry studies indicated that 35–42% of sockeye salmon spawned in the mainstem Kenai River between the Russian River confluence and Skilak Lake. Another 10–20% spawned in an approximately 16 km segment of the Kenai River immediately below Skilak Lake, while 11–21% spawned in upper tributaries of the watershed (Russian River, Quartz Creek, Trail Lakes, Ptarmigan Creek, and others).

Key words: sockeye salmon, *Oncorhynchus nerka*, Kenai River, escapement, abundance, mark–recapture, fish wheel, weir, radiotelemetry, passive integrated transponder (PIT) tag.

INTRODUCTION

The Kenai River late-run sockeye salmon run is typically the largest of 4 major sockeye salmon, *Oncorhynchus nerka*, runs (Kenai, Kasilof, Susitna, and Crescent rivers) in Upper Cook Inlet (UCI; Figure 1). Since 1976, estimated total UCI sockeye salmon runs have ranged from 1.8 to 12.1 million, while estimated Kenai River sockeye salmon runs have ranged from 654,000 to 8.6 million (Tobias and Willette 2004). Within the Kenai River watershed, the majority (~90%) of sockeye salmon fry rear in glacially turbid Kenai and Skilak lakes (DeCino et al. 2004), but significant numbers also rear in Hidden and Russian lakes. The glacial waters of the Snow River feed into Kenai Lake, the outlet of which is the beginning of the Kenai River (Figure 2). Downstream from this lake, the Russian River flows into the Kenai River, and then through the Kenai River canyon and into Skilak Lake. Hidden Creek, the outlet stream of Hidden Lake, flows directly into Skilak Lake. Below Skilak Lake, the river drops through Naptowne Rapids, but then has a relatively low gradient as it flows westerly into UCI. An early (June) sockeye salmon run into the Kenai River spawns in the Russian River watershed, whereas the late-run (July–August) sockeye salmon spawn in several tributaries flowing into Kenai and Skilak lakes, as well as in the mainstem Kenai River between Kenai and Skilak lakes, and in an approximately 6 km segment of the Kenai River below Skilak Lake. Kenai River late-run sockeye salmon are harvested in mixed-stock gillnet fisheries in Cook Inlet and in inriver sport and personal use fisheries. Management of the Kenai River late-run sockeye salmon run is based upon achieving a spawning escapement within a specific escapement goal range. The escapement goal range during this study for Kenai River late-run sockeye salmon was 500,000 to 800,000 (Clark et al. 2007).

The escapement goal range for Kenai River late-run sockeye salmon has been based, in part, upon the number of wild sockeye salmon estimated to spawn within the watershed. The number of wild sockeye salmon spawning within the watershed has been estimated from the total inriver sonar estimate of sockeye salmon minus (1) the estimated number of sockeye salmon harvested in recreational fisheries upstream of the sonar, and (2) the number of hatchery-origin sockeye salmon enumerated at a weir on Hidden Creek (Tobias and Willette 2004). Harvests in recreational fisheries have been estimated annually using a statewide harvest survey (Jennings et al. 2010) and creel surveys conducted during the fishery (King 1995, 1997). Sonars have been operated on the Kenai River at river kilometer (rkm) 31.1 during July and early August since 1968 (Westerman and Willette 2011). Sonar technology has been used because high glacial turbidity precludes visual enumeration of migrating salmon in this river. Prior to 1978, uplooking transducer arrays were used to enumerate salmon, but have since been replaced with side-looking Bendix sonars. Fish wheel catches have been used to apportion sonar counts to species when the fraction of other species in the catches exceeded 5%. This apportionment has typically occurred only in early August during even-numbered years, when pink salmon were most abundant.

The annual Bendix sonar-derived estimates of Kenai River sockeye salmon abundance passing rkm 31.1 have been compared with weir counts (Tarbox et al. 1981), split-beam sonar estimates (Smith and Maxwell 2007), and dual frequency identification sonar (DIDSON)[1] estimates of salmon abundance (Maxwell et al. 2011). In addition, potential biases in the Bendix sonar estimates of sockeye salmon abundance in the Kenai River were investigated by Ehrenberg (1990) following the 1989 *Exxon Valdez* oil spill. While the Bendix sonar was used to count fish that swim through the sonar beams located along both banks of the river, the entire river was not ensonified. In areas with swift currents, sockeye salmon typically swim along the river banks where currents are slower due to friction. However, if some sockeye salmon swim over the top of the bottom-oriented sonar beam or if they pass in the center of the river between the 2 beams, they would likely not be counted resulting in an underestimate of the true abundance. Tarbox et al. (1981) operated side-looking Bendix sonars at rkm 31.1 during June and found that the subsequent catch and escapement of early-run Russian River sockeye salmon accounted for 99% of the sonar estimate. Ehrenberg (1990) concluded that there were no sources of error in the characteristics or operation of the Bendix sonar that would lead to the conclusion that the abundance estimates in 1989 were biased low. Parrish (1999) concluded that the Bendix sonar calibration procedure likely introduced variability into the estimates, and that the system's automatic counter and station operator's manual counting likely became saturated at high salmon densities. Using split-beam sonar, Smith and Maxwell (2007) did not find a consistent bias in the Bendix sonar estimates of salmon passage, but they also concluded that split-beam sonar was not the best equipment to replace the Bendix sonar. Maxwell et al. (2011) concluded that the DIDSON abundance estimates were 1.25 times greater than the Bendix estimates on the south bank and 1.59 times greater on the north bank. The DIDSON sonar estimates were primarily greater than the Bendix estimates at close range where the Bendix beam is narrowest. This project used mark–recapture techniques to independently estimate the abundance of sockeye salmon migrating upstream past the sonars operated at rkm 31.1 in 2006–2008. Since, the Kenai late-run sockeye salmon escapement goal was re-evaluated and expressed in DIDSON units in 2010 (Fair et al. 2010) and DIDSON was used for management in 2011 and will be used for the foreseeable future, we compared our mark–recapture abundance estimates with DIDSON abundance estimates in 2006–2008.

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[1] Product names used in this report are included for scientific completeness, but do not constitute a product endorsement.

OBJECTIVES

1. Conduct mark–recapture experiments in 2006–2008 to estimate the abundance of adult sockeye salmon migrating upstream of rkm 31.1 on the Kenai River during the period of sonar operation and test whether mark–recapture and DIDSON abundance estimates differ from each other; and
2. Use radiotelemetry to determine the distribution of sockeye salmon spawners within the Kenai River watershed, estimate the migratory timing of major spawning stocks past rkm 31.1 and estimate the migration rates of sockeye salmon in the Kenai River in 2006–2008.

METHODS

STUDY DESIGN

Mark–recapture experiments were conducted to estimate the abundance of sockeye salmon in the Kenai River migrating upstream of rkm 31.1 (Figure 2), the location adult sockeye salmon have historically been enumerated using side-looking sonar. Two fish wheels located at rkm 31.1, a point hereafter referred to as the "capture location", were used to mark a sample of sockeye salmon adults in approximate proportion to their abundance as they migrated upstream to spawn. Recapture events consisted of the following (1) scanning the catch of sockeye salmon for marks in 2 fish wheels located at rkm 45.1, (2) scanning the entire population of sockeye salmon passing a weir located on Hidden Creek and (3) scanning the entire population of sockeye salmon passing a weir located on the Russian River. Two mark–recapture datasets resulted from this design. The first was based on fish marked at fish wheels at rkm 31.1 and sampled at the Russian and Hidden lake weirs. Recapturing fish at the weirs had the potential of generating very large sample sizes for marked sockeye salmon, thereby increasing precision of the abundance estimate and allowing powerful testing of experimental assumptions. The second dataset was based on fish marked at the fish wheels at rkm 31.1 and sampled by the recapture fish wheels at rkm 45.1. This study design provided 4 estimates of abundance at rkm 31.1 depending upon the recapture site(s): (1) Russian weir, (2) Hidden weir, (3) weirs combined, and (4) rkm 45.1 fish wheel. This study was designed with redundancy in mind to allow for more than one mark–recapture estimate in the event that any particular estimate was unattainable and as a diagnostic for compliance with mark–recapture assumptions. Theoretically, all estimates should be the same, i.e., any differences among them should only be due to sampling error.

Fish wheel (rkm 45.1) and weir recapture data were segregated in the analyses. The mark–recapture estimators used in this study were not structured to use data from fish sampled twice, because tagged fish recaptured in the fish wheels at rkm 45.1 were sacrificed to verify the presence of the tag.

A subset of the sockeye salmon captured by the fish wheels at rkm 31.1 were marked with a PIT (Passive Integrated Transponder) tag or radio transmitter. Each PIT and radio tag had a unique code allowing us to identify each fish when it was recaptured. Each tagged fish also had their adipose fin removed and their sex and length measured. We attempted to apply PIT tags and radio tags in approximate proportion to abundance.

Fish with transmitters were monitored by fixed and mobile receiver stations to: (1) determine the proportion that migrated upstream of the capture location past the recapture fish wheels at rkm 45.1 and above Naptowne Rapids at rkm 63.7, and (2) obtain migratory timing, migration speed, and spawning distribution information. The proportion of radio tags migrating past the recapture fish wheels at rkm 45.1 was used to estimate the proportion of all marked fish (both radio and PIT tagged) that migrated upstream of the capture location and were vulnerable to recapture in the fish wheels; i.e., the proportion that did not succumb to effects of capture and handling. The proportion of radio tags migrating above Naptowne Rapids at rkm 63.7 was used to estimate the proportion of all marked fish that migrated upstream of the capture location and were vulnerable to recapture at the Hidden Creek and Russian River weirs. The number of PIT tags applied was then discounted accordingly. Sockeye salmon caught in the fish wheel recapture event were visually examined for an adipose clip, and those with an adipose clip were scanned with an electronic PIT tag reader for the presence of a tag. Fish recaptured at the Russian and Hidden Lake weirs were scanned automatically by PIT tag readers attached directly to each weir. The total number of fish examined for marks in the recapture events, and the number and tag codes of recaptured marked fish were recorded. At the rkm 45.1 fish wheels, length was measured on all recaptured fish and on a sample of unmarked fish. Length was measured and age, sex and length determined for a sample of fish passing through the weirs.

Additional data were collected to test model assumptions or to mitigate violations of them. These included application of radio transmitters to adjust for handling and tag-induced mortality at the marking site (described above), application of secondary marks to assess tag loss, and collection of fish length data at fish wheels and weirs to test for size-selectivity. Drift gillnetting was also conducted in the center of the river channel at the recapture fish wheels to estimate the marked fraction of any sockeye salmon migrating mid-river. Other information collected during the study included genetic data from marked fish (via sampling of axillary processes), pertinent to the Russian River run reconstruction project.

MARKING EVENT

Sockeye salmon were captured for tagging at our rkm 31.1 sonar site using 2 fish wheels located on each bank of the river. The fish wheel on the north bank was located approximately 150 m below the sonar, a site where it has been operated over the past 10 years. The fish wheel on the south bank was located approximately 1,000 m upstream of the sonar. This site was chosen, because a fish wheel had been successfully operated in this area during a previous coho salmon tagging project (Robert Massengill, Sport Fish Biologist, ADF&G, Soldotna; personal communication). Weirs were installed between the fish wheels and the river bank to force fish to swim within the zone swept by the fish wheel baskets. Use of weirs had been previously shown to increase salmon catches. Fish wheel installation and testing was conducted during the last week of June, so that we could begin tagging on July 1.

Although, rkm 31.1 sonars typically begin operation on July 1 each year, our mark–recapture estimates of sockeye salmon abundance apply only to periods when fish were being tagged, i.e., July 3–August 24, 2006, July 1–August 23, 2007, and July 7–August 17, 2008. In 2006, fish wheels began operation on July 1, but no fish were tagged until July 3 due to very low catches. In 2008, low and very clear water precluded effective fish wheel operation until July 7. Fish were tagged until the end of sonar operations in 2007 and 2008, but in 2006 no fish were tagged after August 24, because many of the technicians we hired to tag fish were students that needed to return to school before the end of August. Sonar operations in 2006 continued until August 31 due to the very late sockeye salmon run that year (Westerman and Willette 2007).

In 2006, we anticipated applying 7,000 PIT tags to sockeye salmon based upon an assumed total passage of 700,000 sockeye salmon during the period of normal sonar operations and a 1% tagging rate. Fish were tagged over an 18 hour period each day to enhance the likelihood of proportional tagging. Both fish wheels were operated almost continuously between 0800 and 0200 the following morning to concentrate effort during the period when most sockeye salmon appeared to move in the Kenai River (Figure 3). Three crews of 3 people operated the fish wheels during two 9 hour work shifts each day. Crew schedules were staggered throughout the week to maintain tagging operations 7 days a week. Initially, the number of fish tagged each hour on each bank was expected to be 1% of the hourly sonar count for that bank from the previous hour. The crews alternated tagging fish between the 2 banks approximately every hour to minimize holding time of fish in the fish wheel live boxes. If the crews could not tag the desired number of fish during a given hour, additional tags were to be applied the following hour to achieve the desired tagging rate. During the last hour (0100–0200) and the first hour of tagging the next morning (0800–0900), the number of tags applied increased to compensate for tags not applied from 0300–0800. However, after the first 3 weeks of tagging we found this method was not workable, because low fish wheel catches during the first 3 weeks precluded us from tagging 1% of the sonar count. Once the run increased, fish wheel catches increased but our tagging crew could not physically tag enough fish to maintain a 1% tagging rate. Therefore, on approximately July 20 the crews were instructed to alternate tagging fish between the 2 banks each hour and tag as many fish as possible.

In 2007, we anticipated applying 8,000 PIT tags based upon the number of PIT tags applied in 2006 and expected increases in the number applied due to changes in crew schedules. Three crews of 3 people operated the fish wheels during two 8 hour work shifts each day. Prior to the peak of the run (approximately July 1–20), crews started tagging at 1000 and ended at 0400 the following morning. This schedule was expected to maximize the number of fish tagged prior to the peak of the run when low fish wheel catches limited the number of fish tagged (Figure 3). When fish wheel catches increased to the point that crews could not tag every sockeye salmon caught in the wheels, the schedule was changed to a start time of 0800 and an end time of 0200 the following morning. This schedule limited the amount of time crews worked in the dark which could affect data quality, but it did not reduce the number of fish tagged due to the high catches at this time. Throughout the season, crew schedules were staggered during the week to maintain tagging operations 7 days a week. Prior to the peak of the run, tagging crews alternated between fish wheels approximately every hour, tagging all fish caught. During this time, fish wheels were left running during meal breaks. The numbers of fish accumulating in the trap box during this period was typically very low (<10 fish). When fish wheel catches increased during the peak of the run, crews alternated between fish wheels approximately every 2 hours, and the wheels were turned off when crews were not present tagging fish. During this period of high catches, sockeye salmon were taken directly out of the fish wheel basket or trap box and tagged as quickly as possible.

The tagging crew schedule developed in 2007 was applied again in 2008, except the PIT tagging rate after August 1 was adjusted to better match the tagging rate in July. The expected number of PIT tags to apply in August was calculated by taking the ratio of the number of PIT tags applied to the total DIDSON count in July and multiplying by the projected DIDSON count in August. PIT tags were then applied to every n^{th} sockeye salmon captured in the fish wheels. The nth tagging rate was calculated by dividing the expected number of PIT tags to apply in August by the expected August fish wheel catch.

PIT tags were used in this study because they are small, quick to apply, not visible externally (to avoid enhancing predation), internal (no hydrodynamic drag), uniquely numbered, can be identified automatically, and can be scanned without handling the fish. PIT tags are constructed with an integrated circuit chip connected to a tightly wound copper hoop antenna. The tags can be interrogated by a 134.4 kHz signal from a scanning device. When the scanning device frequency excites the PIT tag, the tag emits a signal back to the receiver with a unique code (10-digit hexidecimal code displayed alphanumerically). The PIT tags are encapsulated in glass and are typically 12 mm long by 2.1 mm wide (about the size of a grain of rice). PIT tags have been used extensively in research on salmonid survival (Prentice 1990; Skalski et al. 1998), movement (Prentice et al. 1990c; Hildebrand and Kirschner 2000), behavior (Brannas et. al. 1994), and estimation of population size (Willette et al. 2003). Prentice et al. (1990a) found that when properly injected into the body cavity, PIT tags are retained at high rates (100% and 99.7% in male and females, respectively), and that tag-induced mortality was low. Prentice et al. (1990b) described a PIT-tagging method suitable for Columbia River salmon and Prentice et al. (1990a) noted that all wounds to maturing Atlantic salmon that were PIT tagged using this method were closed and healing by the third day. Prentice (1990) compared juvenile Chinook salmon and steelhead trout that were PIT tagged with cold branding, coded wire tagging, and a control group (handling but not tagged) at dams on the Columbia River. He noted no significant increased mortality of PIT tagged fish when compared to these other tagging methods.

Three people per crew were necessary to quickly process each sockeye salmon captured to reduce handling time and associated stress. Captured sockeye salmon were placed in a holding tank onboard a riverboat prior to tagging. Fish that were severely injured were not tagged. A bucket was used to frequently add fresh water to the tank. A padded, plastic cradle device was slipped around the fish to restrain it during tagging. One person held the restrained fish and the other inserted a PIT tag into the cheek using a hypodermic needle and syringe. The crew removed the adipose fin, determined sex, and measured fork length (MEFT, from the mid eye to the fork of tail) to the nearest 5 mm using a meter on the cradle. Removal of the adipose fin served to identify PIT tag loss between the capture and recapture events and served as the primary mark at the recapture fish wheels at rkm 45.1. Tagged fish were passed through a tag detection antenna (Biomark Inc®) to verify that a PIT tag was present in the cheek. The PIT tag reader was interfaced with a handheld computer (Allegro CX). The PIT tag code for each tagged fish was automatically written to a file in the handheld computer along with the date and time. A crew member input the riverbank, sex and length of the tagged fish into the computer using a custom data entry program. Whenever possible, sockeye salmon were taken directly out of the fish wheel basket and tagged immediately. Radiotelemetry data for coho salmon indicated that fish that were tagged immediately upon capture experienced a mortality rate one-half that of fish held for variable times in the fish wheel trap box before tagging (10% versus 20% mortality, Carlon and Evans 2007).

Established methods (Tobias and Willette 2004) were used to collect scale samples for age determination from every sixth PIT-tagged fish tagged on each bank. A tissue sample (axillary process) was also collected from every PIT-tagged fish sampled for age determination and placed in a uniquely numbered vial for later genetic stock identification. This sampling rate was designed to provide the number of genetic sample needed for the Russian River run reconstruction project. The handheld computer prompted the crew to collect the scale and genetic samples.

We anticipated applying esophageal radio transmitters to approximately 200 sockeye salmon each year. We attempted to apply radio transmitters in approximate proportion to sockeye salmon abundance by using historical sonar run timing data (2000–2004) to calculate the number of radio tags to apply each day. Within a day, the number of radio tags to apply on each bank was based upon the proportion of the previous day's total sonar count on each bank. Within each bank, the previous day's sonar count was divided by the number of radio tags to be deployed to determine that every n^{th} fish shall be radiotagged. Within each bank, the first fish to tag each day was randomly selected from the first n fish and every nth fish thereafter during that day was radiotagged.

We used model F1840B radio transmitters manufactured by Advanced Telemetry Systems, Inc. (ATS) operating on 20 frequencies within the 151.100 megahertz (MHz) to 153.000 MHz range. Each transmitter was equipped with a mortality indicator mode that activated when the tag was motionless for approximately 4 hours. Transmitters were about 56 mm long, 17 mm in diameter, weighed 22 g in air, contained a 30 cm external whip antenna, and had a warranty life of at least 122 days. Radio tags were inserted through the esophagus and into the upper stomach of the fish using an approximately 25 cm polyvinyl chloride (PVC) tube with a diameter equal to that of the radio tag. The radio transmitter was seated on the end of the tube. The antenna was threaded through the tube and gripped to hold the tag in place. The radio transmitter was then pushed through the esophagus and seated such that the antenna end of the radio tag was 0.5 cm beyond the base of the pectoral fin. The PVC tubes were marked with reference points to assure proper tag insertion depths. At the beginning of each season, a few sockeye salmon of varying sizes that were radiotagged were killed and necropsied to verify proper tag placement in the stomach. Sockeye salmon <400 mm MEFL were not radiotagged to minimize handling mortality. Only 0.1–0.3% of sockeye salmon captured in the rkm 31.1 fish wheels were <400 mm MEFL. The frequency and pulse code of each radiotagged fish was entered into the handheld computer using the same program used for normal PIT tagging operations. All marked sockeye salmon were released into the river adjacent to each fish wheel immediately after all data were recorded.

Recovery Event Fish Wheels

The first recapture event consisted of scanning the catch of sockeye salmon for marks in 2 fish wheels located at rkm 45.1. The location of the recapture fish wheels was chosen largely because it is where these same fish wheels have been operated in August and September to provide an index of the run of adult coho salmon to the Kenai River.

Each sockeye salmon removed from the fish wheel was first examined for the presence of an adipose fin. If the adipose fin had been recently removed, fish were scanned with a handheld PIT tag reader. If a tag was detected, the tag code was recorded in the PIT tag reader memory and written on a data form. If a PIT tag was not detected, the fish was sacrificed to verify that a PIT tag was not present. If the adipose fin had been recently removed, the fish was also examined for the presence of a radio tag antenna, and the presence\absence of the antenna was recorded on the data form. Periodically, a MEFL was measured on a sample of unmarked fish. When combined with lengths of marked fish, these data were used to test for size-dependent capture probability. All efforts were made to minimize capture and handling-induced stress at the recapture location. The possible states of fish in the fish wheels and actions taken are summarized in Table 1.

Excluding time for meal breaks and shift changes, both fish wheels operated continuously, 24 hours a days, 6 days a week from July 1 through August 25 and then at a lower rate until September 30. Three crews of 2 people each operated the fish wheels during three 8-hour work shifts per day. The fish wheels were started one-half hour after the shift started (0630, 1430 and 2230, respectively) and stopped one-half hour before the shift ended (1330, 2130 and 0530, respectively). This allowed adequate time to travel to or from the launch site, launch or secure the boat, equipment, and data forms, and to travel by boat to or from the fish wheels. The actual time at which each fish wheel was stopped at the end of each shift depended on catch rates. When the catches were low, both fish wheels operated, and the crew sampled fish as they were caught, switching to the other fish wheel approximately every 45 minutes. When catches were high, only one fish wheel operated at a time to avoid having too many fish accumulate in the live box. Fish wheel operations ceased at a time that ensured that all captured fish were sampled and released by about one-half hour before the shift ended. Two people per crew were needed to quickly process each sockeye salmon captured to reduce handling time and associated stress. The number of fish of other species captured was also recorded, as well as the date, location, and time of capture.

Drift gillnetting was conducted 2 days each week at the rkm 45.1 fish wheel site. Gillnetting was conducted on Tuesdays and Thursdays, with one morning shift (0600–1400) on one day and an afternoon shift (1400–2200) on the other day. Morning and afternoon shifts were rotated within each day. Gillnets were drifted between the north and south bank recapture fish wheels. The gillnets were 10 m long and 3 m deep (30 meshes) with a 4.75 in stretched multifilament (SMS-38) web. The crew attempted to drift the net no closer than 20 m from either shore to avoid capturing salmon that were migrating along the shoreline and thus vulnerable to capture in the fish wheels. A rangefinder was used periodically to measure the distance from shore. The net was retrieved into the boat when 5 fish had been captured or the boat had drifted out of the sampling area (adjacent to the lower fish wheel). The net was retrieved into the boat with the fish remaining entangled to avoid capturing too many fish as the net drifted out of the sampling area.

After the net was retrieved, each fish was removed from the gillnet. Sockeye salmon were inspected as described for fish wheel captures. The crew tallied the number of fish caught in the gillnet by species and recorded this data. No sockeye salmon captured in gillnets were marked with a PIT or radio tag.

RECOVERY EVENT WEIRS

A second recapture event consisted of scanning sockeye salmon for marks as they passed through weirs located on Hidden Creek and Russian River. Electronic PIT tag detection systems were employed on both weirs to scan all fish passing through the weirs for tags. Rectangular 12x31.5 inch PIT tag antennas were affixed to the upstream gate on the live box at Russian River weir and to a gate in the weir at Hidden Creek. A plywood chute was constructed on both gates to ensure that the antenna was at least 24 inch from any metal weir parts. A PIT tag reader was housed in an aluminum box and attached to the antenna by a 20 ft cable. The PIT tag detection system was powered by 2 external 12V batteries attached to a sonar panel on a mast. The aluminum electronics box, the mast, and solar panel were surrounded by an electric fence to minimize tampering by wildlife. In 2007 and 2008, a second PIT tag antenna system was attached upstream of the plywood chute on each weir. An approximately 2 m Vexar chute led fish from the first antenna through the second antenna. This redundancy in the PIT tag detection system allowed us to calculate the detection rate of both antennas assuming the detection rates of the 2 antennas were independent.

Technicians maintained PIT tag readers and conducted tag detection tests at each weir each day during operation. Prior to daily fish passage each day, the PIT tag reader was placed within the aluminum box on the weir, the antenna and power cables attached, and the reader turned on. A visual inspection of the cables and antenna was conducted and any damage recorded (e.g., loose antenna, error messages on the reader, water damage, etc.). The voltage on the external batteries was tested and the batteries replaced with a newly charged one if the voltage dropped below 12V. The date, time, any problems with the reader, battery voltage, and whether the battery was replaced were recorded on a data form.

Prior to daily fish passage each day, technicians conducted tag detection tests to estimate the PIT tag detection rate at the weir. Tag detection tests consisted of passing fifty 20-ml plastic vials, each containing a PIT tag through the rectangular PIT tag antenna one at a time, collecting the bottles, then passing all 50 through the antenna again, one at a time. The bottles contained varying amounts of water so their buoyancies varied, causing the bottles to naturally explore all areas of the detection field as they passed through the antenna. In 2007 and 2008, detection rates were calculated for each antenna separately and both antennas combined.

All fish enumerated through the weir passed through the PIT tag antenna system. Prior to passing any fish, the electric fence surrounding the antenna (used to ward off bears) was turned off to minimize any noise that might affect tag detection.

At the end of each day, the PIT tag reader was removed from the aluminum box and taken into the cabin. In the cabin, a custom program was run on a laptop computer to download data from the PIT tag reader to a text file. The program calculated the detection rate from the test conducted that morning, and wrote the number of PIT tags detected (not from detection test) and the detection rate for that day to a text file.

Each day during morning radio check, the weir crew reported the following data from the previous day: (1) PIT tag detection rate, (2) number of PIT tags detected (not from detection test), (3) total sockeye salmon counted, and (4) any problems with the PIT tag equipment and any needed equipment or help. PIT tag detection rate, number of PIT tags detected, and number of sockeye salmon counted each day, etc. were recorded in a spreadsheet in Soldotna and stored on our local area network.

The weir crews and Soldotna staff monitored tag detection rate data, and if 95 or more trials were correctly detected (95% detection rate), the detector was considered fully functional. If the detection rate was less than 95%, action was taken to determine the cause of the problem, and the PIT tag detection system was then either repaired or replaced. While the detector was being repaired or replaced, the crew passed fish normally and no scanning for PIT tags occurred. The numbers of fish passed on these days were subtracted from the total weir count when calculating the tagged to untagged ratio of sockeye salmon passing through the weir.

RADIO TAG RELOCATION

The movements of radiotagged fish were monitored primarily by a series of fixed, land-based, radio-receiving stations. Fixed station data were supplemented and verified by data collected during mobile tracking surveys conducted by boat and fixed-wing aircraft. In 2006–2008, 6 land-based stations were operated at riverbank locations along the Kenai River at (1) rkm 31.1

(rm 19.5 – capture location and sonar site), (2) rkm 45.4 (rm 28.2 – to monitor fish migrating past the recapture fish wheels), (3) rkm 76.5 (rm 47.5 – near Lower Olsen Creek) to monitor fish migrating into the Skilak Lake outlet spawning area, (4) rkm 80.5 (rm 50.0. – Skilak Lake outlet) to monitor fish migrating out of the Skilak Lake outlet spawning area, (5) rkm 104.6 (rm 65.0 Skilak Lake inlet) to monitor fish migrating into the upper Kenai River and (6) rkm 131.2 (rm 82 Kenai Lake outlet) to monitor fish moving into Kenai Lake (Figure 2). In 2007–2008, a seventh land-based station was added at rkm 121.3 (rm 71.0 Jim's landing) to monitor fish migrating up through the Kenai River canyon. Fixed radio-receiving stations were located in the Skilak Lake outlet spawning area to better estimate the proportion of all radiotagged sockeye salmon that utilized this spawning area and to estimate their stream life.

Prior to the first radio tag release, the range at which each station could detect a tag was tested using a tethered radio tag deployed from a boat. The system was adjusted or relocated if necessary to ensure that (1) the detection range was sufficient for a tag to be detected multiple times as fish moved past the fixed station, and (2) no contiguous zones existed within the river channel where tagged fish could escape detection.

At each fixed station, the radio receivers, manufactured by ATS (Model R4000 or Model 4100), were interfaced with a Model 5041 data collection computer (DCC II). The receiver/DCC combination recorded the date, time, and unique frequency/pulse code combinations of transmitters when they were detected. The DCCs continually scanned the frequencies of all transmitters 24 hours per day. Two antennas were coupled with each fixed-station system using an ATS antenna switch (Model 200). One antenna was oriented in a downstream direction, the other in an upstream direction. Signal strength and time of reception was recorded separately for each antenna to provide information on direction of travel.

Mobile systems were mounted in a boat and fixed-wing aircraft. Model 4100 receivers were used alone or interfaced with a DCC. The DCC device was used when large numbers of transmitters were on-air. The DCC was capable of uniquely identifying 3–6 radio transmitters when the transmitters were in close proximity to each other. When tracking with the receiver alone, visual and audible cues produced by the receiver were monitored by the operator. When a cue indicated that a transmitter had been detected, the operator recorded the date, time, frequency/pulse code, and location (to nearest 0.1 river mile from a boat and nearest 0.5 river mile from aircraft). The frequency was displayed on the receiver LCD screen by default. Momentarily adjusting the interval switch to "INT" ("interval") displayed the pulse code, thereby completely identifying a unique radio tag (frequency/pulse code combination).

In 2006, radio tracking surveys were conducted in the mainstem of the Kenai River each week throughout the season using an outboard-powered riverboat. In 2007–2008, radio tracking surveys of the mainstem Kenai River were generally conducted twice per week. This form of tracking allowed for precise relocations of radiotagged fish, confirming data collected by fixed stations. In addition, boat-based tracking in the mainstem downstream from rkm 31.1 (downstream of sonar site) served to verify the fates of fish that moved downstream after tagging.

Fixed-wing aircraft radiotelemetry surveys of the Kenai River watershed were conducted 2–4 times each season. Aerial radio tracking was used to identify fish spawning locations and determine if fish carrying transmitters were capable of reaching spawning destinations (to substantiate the assumption that radiotagged fish are representative of the population of untagged fish). The flights covered the major tributaries and the mainstem Kenai River. The Model 4100 receiver was interfaced with a DCC and monitored by an operator in the aircraft. Each wing strut of the aircraft was fitted with an external antenna. Prior to each flight the DCC was programmed with the 20 study frequencies. As individual frequencies were identified the pulse code was determined and recorded. Each transmitter was located to the nearest 1.0 rkm. Any transmitters signaling a mortality pulse were noted.

Data recorded by each fixed radiotelemetry station was downloaded onsite each week using a handheld or laptop computer. The data were then transferred to a desktop computer located at the ADF&G office in Soldotna and stored on our local area network. All other transmitter detection data from angler recoveries, etc. were recorded in a spreadsheet.

In addition to locations detected from telemetry surveys, final radio tag locations were also collected from miscellaneous sources. Press releases and signs posted along the river and in area sporting goods stores informed anglers and the general public about the project and the importance of returning (or at least reporting) radio transmitters that they recovered during sport fishing efforts. Date, location, and radio frequency/pulse code of recovered marked sockeye salmon were recorded whenever possible.

Radiotelemetry data from each year was archived in a Microsoft Access database that incorporated all data from telemetry surveys, fixed stations, and miscellaneous sources. The database was structured to allow the user to construct a chronological history of detections of each radiotagged fish at fixed stations, during boat or aerial surveys, or returns from fishermen.

DATA ANALYSIS ESTIMATION OF ABUNDANCE

If assumptions 1–5 below were met, then Chapman's modification of the Petersen model (Seber 1982) was used to estimate abundance $\hat{N}$ for an experiment such that:

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

where n_1 is the number of fish captured and marked during event 1, n_2 is the number of fish inspected for marks during event 2, and m_2 is the number of n_2 that possessed marks applied during event 1. The variance of the abundance estimate was estimated as:

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

The conditions necessary for equation 1 to provide an accurate estimate of abundance were described in Seber (1982) :

1. Closed population (i.e., no mortality or recruitment),
2. Either the probability of capture (tagging) was constant across all individuals at the time of capture (constant p_1), or marked fish mixed uniformly with unmarked fish before the recapture event, or the probability of capture was constant across all individuals at the time of recapture (constant p_2),
3. Marking did not affect catchability,
4. Tags were not lost,
5. All tags were recognized and reported.

Assumption 1: The proportion of radio tags released at rkm 31.1 failing to travel upstream (dropouts) was used to discount the number of PIT tags released at rkm 31.1 for deaths due to the tagging process, i.e.,

$$n_1 = \left(1 - \frac{dropouts}{radio\ tags\ released}\right) \cdot PIT\ tags\ released\ . \tag{3}$$

Our reasoning was that if radiotagged fish, which were also given PIT tags and therefore were more insulted than fish receiving only PIT tags, survived the tagging process and continued migration, then chances were at least the same proportion of PIT-tagged fish continued migration as well. If anything, we may have overestimated dropouts of PIT-tagged fish causing our mark–recapture estimate to be biased low. For the abundance estimate derived from tag recaptures at the rkm 45.1 fish wheels, we used an estimate of the survival of radiotagged fish successfully migrating past the fixed station at this location. For abundance estimates derived from tag recaptures at weirs, we used an estimate of the survival of radiotagged fish that successfully migrated above Naptowne Rapids at rkm 63.7 (Figure 2). This approach assumed that there was no spawning below rkm 63.7, so any radiotagged fish that did not successfully migrate above Naptowne Rapids likely succumbed to the effects of tagging; whereas, fish that ceased migrating above Naptowne Rapids may have died after spawning. In both cases, the number of radiotagged fish harvested below either rkm 45.1 or 63.7 (and reported to us) was subtracted from the total number of radio tags released. We further assumed natural and fishing mortalities were equal between tagged and untagged fish, so our abundance estimate was pertinent to the tagging site at rkm 31.1. Note that PIT tags recovered at the rkm 45.1 fish wheels were culled from the experiment using the weirs.

Assumption 2: We attempted to apply tags in approximate proportion to abundance; however, sampling crews became saturated as in river abundance increased causing the probability of capture (tagging) to change over time and therefore among individuals (Figures 4–5). Furthermore, fish wheels are known to exert differing catchabilities over fish sizes (Meehan 1961), and thus we anticipated that the initial capture probability (p_1) would be inconsistent across individuals of different sizes. Furthermore, we did not expect complete mixing of fish to occur as tags deployed later during the run had little to no chance of mixing with fish passing earlier in the run. With respect to probability of capture at time 2 (p_2) at the rkm 45.1 fish wheels, the same inconsistencies as described for p_1 likely occurred with respect to catchability. However, using weirs as recapture sites, recapture probability was equal to 1.0 at all weirs or equal to zero at other sites.

For the above reasons, we relied on both length and temporal stratification to reduce the bias of the estimate using the rkm 45.1 fish wheels as the recapture site. However, only length stratification was used to reduce the bias of the estimate when weirs were used as the recapture site. Temporal stratification was used in the Darroch model (see model selection *Methods* below) to incorporate changes in movement and capture probabilities through time, when p_1 and p_2 were inconsistent across temporal strata. But as fish cannot move between length categories, separate estimates were required for each length stratum. Chi-square tests have long been relied upon to help decide whether to pool or separate strata during mark–recapture studies (Seber 1982, Schwarz and Taylor 1998). Following Clark (1991), we expanded this idea by using maximally selected chi-square values to determine cut points for strata.

The following table was used to separate fish into length strata:

	Small	Large
Marked	m_{2Small}	m_{2Large}
Not marked	n_{2Small}- m_{2Small}	n_{2Large}-m_{2Large}

The split was made between length groups if the maximum chi-square was significant (α = 0.05). Then, the process was repeated within the small and large strata to see if further stratification was required. The strategy was to choose strata that homogenize p_1 at the tagging site within each length stratum. A separate mark–recapture analysis was performed for each length stratum.

For the case where the rkm 45.1 fish wheels were used as the recapture site, the following tests were conducted within each length stratum to identify temporal tagging strata by finding cut points that maximized the chi-square performed on the following table:

Tagging	Rkm 45.1 fish wheels		
stratum	Early	Late	Not seen again
Early	$m_{2Early,Early}$	$m_{2Early,Late}$	n_{1Early}- m_{2Early}
Late	$m_{2Late,Early}$	$m_{2Late,Late}$	n_{1Early}- m_{2Late}

Schwarz and Taylor (1998) recommended this test for determining whether to pool 2 consecutive tagging strata. The split was made between dates if the maximum chi-square was significant (α = 0.05). No more than 2 temporal strata per size stratum were used as more strata did little to improve accuracy or reduce precision. Temporal recovery strata were determined by lagging the cut point dates by the average travel time to the recapture site. The strategy was to choose strata that homogenize movement probabilities within each temporal stratum. In addition to this technique, visual inspection of m_2/n_1 plotted against marking date helped us to recognize changes in capture probabilities over time. Occasionally, this plot was used to identify cut points different than that which maximized the above chi-square.

Assumption 3: Validating this assumption was not possible for the recapture site at rkm 45.1, beyond determining the proportion of tagged fish that succumbed to tagging, an extreme effect of tagging on catchability. Assumption 3 was more likely met for weir recapture sites since the probability of capture was 100% at both weirs.

Assumption 4: The adipose fin was removed on all pit-tagged fish, resulting in 2 marks per fish. Pit tag loss was determined by observing the number of fish at rkm 45.1 missing adipose fins and not possessing pit tags. The tag loss rate (π) was estimated as:

$$\pi = \frac{\textit{number of adipose clipped fish with no pit tag}}{\textit{all fish with adipose clips}}, \tag{4}$$

and the number of recaptures (m_2) was divided by (1- π) to correct for tag loss. Uncertainty surrounding this estimate was ignored as it was considered small compared to the overall uncertainty in m_2.

Assumption 5: We were unable to quantify how many tags went unreported at the rkm 45.1 fish wheels. However, tag detection tests at weir sites indicated that detection rates were near 100%, so we assumed that all tags were reported. Abundance estimates would be biased high if this assumption were violated.

Model Selection

For the case where the rkm 45.1 fish wheels were used as the recapture site, one of 2 models (Schwarz and Taylor 1998) were chosen (Arnason et al. 1996) to provide a mark–recapture estimate within length strata: (1) Chapman's modification of the pooled Petersen (PPE) or (2) partially stratified Petersen (i.e., the Darroch model; Darroch 1961), depending on whether assumption 2 above was met. The PPE was chosen when a non-significant (α = 0.05) chi-square resulted from any of the following tests:

Mixing test(p_2)

Tagging stratum	Recovered	Not seen again
Early	$m_{2Early,.}$	$n_{1Early} - m_{2Early}$
Late	$m_{2Late,.}$	$n_{1Late} - m_{2Late}$

Equal proportions test(p_1)

	Early	Late
Marked	$m_{2.,Early}$	$m_{2.,Late}$
Not marked	$u_{2.,Early}$	$u_{2.,Late}$

where, u_2=number of fish without tags in the second sample (n_2).

For the case where weirs were used as recapture sites, recapture probabilities were equal (p_2=1.0) among all sampled strata, so there was zero correlation between tagging and recapture probabilities, resulting in no bias using the PPE (Schwarz and Taylor 1998, page 288). In these cases, estimates were only stratified by length and separate PPE analyses were performed for each length stratum.

Comparison of Abundance Estimates

We used the *Z-test* statistic (Springhall 2003) to test whether our mark–recapture and DIDSON abundance estimates were significantly different. We assumed that the variance of DIDSON estimates resulted only from the 10minute subsampling procedure used at the 31.1 rkm sonar site (Westerman and Willette 2011). Woody (2007) estimated that a 10minute subsampling procedure every hour resulted in an approximately 5% relative error in salmon abundance estimates. Separate *Z-tests* were conducted for each length stratum and for all length strata combined. We also used the *Z-test* statistic to test whether our mark–recapture abundance estimates from the Russian River and Hidden Creek weirs sites were significantly different for those length strata available at both weir sites. These tests evaluated Schwarz and Taylor's (1998) conclusion that zero correlation between tagging and recapture probabilities should result in no bias using the PPE, i.e., any difference between abundance estimates should only be due to sampling error.

Data Analysis Radiotelemetry

We estimated the mean migration time (number of days) and migration speed (km day^{-1}) of radiotagged sockeye salmon swimming between 5 fixed radiotelemetry stations located at rkms 31.1 (sonar site), 45.1 (recapture fish wheels), 80.5 (Skilak Lake outlet), 104.6 (Skilak Lake inlet), and 132.0 (Kenai Lake outlet) during 7 weekly time periods (Figure 2). Eight analyses of variance were conducted to test for differences among the weekly mean migration times and speeds between the 5 fixed radiotelemetry sites. The dependent variables were migration time and speed and the independent variables were tag week.

We estimated the run timing of radiotagged sockeye salmon passing rkm 31.1 and later relocated in 4 major spawning areas in the Kenai River watershed. The highest location of each relocated radiotagged fish in the watershed was used to infer probable spawning destination. For each of the 4 spawning areas (k), we estimated the weekly proportion (p_{ik}) of the total number of recovered radio tags (m_{ik}) from weekly release strata i where

$$p_{ik} = \frac{m_{ik}}{\sum_i m_{ik}} \quad . \qquad (5)$$

To correct for apparent unequal tagging proportions among release strata, the number of recovered radio tags in each release stratum (m_i) was weighted (w_i) by the weekly DIDSON estimate of sockeye salmon passage at rkm 31.1 (Nd_i) and the inverse of the proportion of tags used in each release stratum (Willette et al. 2003) such that:

$$w_i = \frac{Nd_i \big/ \sum_i Nd_i}{m_i \big/ \sum_i m_i} \quad . \qquad (6)$$

DIDSON estimates of sockeye salmon passage were used to weight the radio tag recoveries because this abundance estimate likely represented actual sockeye abundance more than fish wheel catch per effort. As a measure of stock-specific run timing past rkm 31.1, the weighted weekly proportion (pw_{ik}) of the total number of recovered radio tags from release strata i found in spawning area k was estimated as:

$$pw_{ik} = \frac{w_i m_{ik}}{\sum_i w_i m_{ik}} \quad . \qquad (7)$$

The simple proportion of the total number of relocated radio tags found in 24 zones in the watershed provided an approximate measure of probable spawner distribution.

RESULTS

ABUNDANCE

2006

In 2006, we were unable to apply PIT tags in proportion to the daily sonar estimate of sockeye salmon passage due to variable fish wheel catchability and sockeye salmon run timing. Prior to July 16, fish wheel catches were very low, presumably due to high water clarity and low fish wheel catchability (Figure 4). Sonar data during that period indicated that sockeye salmon were distributed offshore of the narrow near shore zone sampled by the fish wheels. After July 16, sockeye salmon distribution shifted closer to shore and fish wheel catches increased. After July 21, the run increased (Figure 4), and crews were unable to tag 1% of the daily sonar count due to the large numbers of fish. The number of hours the fish wheels operated during the peak of the run was substantially reduced because crews could not handle all the fish caught each hour (Figure 4). Our tagging operation terminated on August 25 because many tagging crew members needed to leave. Normally, this would not have been a problem, but the sockeye salmon run in 2006 was the latest ever observed on the Kenai River.

In 2006, we applied PIT tags to 6,901 (350–650 mm) and radio tags to 215 (460–625 mm) sockeye salmon at rkm 31.1 between July 3 and August 24. Substantially more PIT tags were applied on the north bank (4,180) than the south (2,720) bank. Ninety-five percent of radio tagged sockeye salmon migrated past the rkm 45.1 fish wheels, and 89% migrated upstream of Naptowne Rapids at rkm 63.7 (Table 2, Appendix A1). Estimated tagging-induced mortalities to rkm 45.1 (5%) and 63.7 (11%) were significantly (P<0.05) different. We examined 59,609 fish (370–699 mm) for tags at the rkm 45.1 fish wheels, and 89 PIT-tagged sockeye salmon were recaptured. At the Hidden Creek weir, 36,138 (470–569 mm) sockeye salmon were scanned for tags, and 185 PIT tags were detected. At the Russian River weir, 85,924 (370–629 mm) sockeye salmon were scanned for tags, and 156 PIT tags were detected. The daily number of PIT tags detected passing through Hidden Creek and Russian River weirs increased relative to the number of fish scanned for tags later in August (Figure 5). The size frequency distributions of untagged sockeye salmon were estimated with samples collected at rkm 45.1 fish wheels (n=3,528), at Hidden Creek weir (n=914), and at the Russian River weir (n=201).

No tag loss was detected among the freshly adipose-clipped sockeye salmon recaptured in the rkm 45.1 fish wheels. Tag detection was not independently estimated at the rkm 45.1 fish wheels, but our crews reported that some tags were probably overlooked, particularly at night and during the peak of the run when very large numbers of sockeye salmon were scanned. The very low numbers of recaptured tags at this site during the peak of the run were consistent with this concern (Figure 5). The abundance estimate derived from tags recaptured at the rkm 45.1 fish wheels was therefore dismissed, because it was likely biased high due to poor tag detection (Table 3). However, daily tests indicated that tag detection was >95% on 89% and 96% of the days at Hidden Creek and Russian River weirs, respectively.

Initial capture probabilities (p1) generally increased with fish length up to 569 mm (Figure 6). Chi-square tests identified 4 length strata corresponding with changes in initial capture probabilities (Table 3). The same 4 length strata were used for the abundance estimates derived from tag recaptures at the 2 weir recapture sites. However, the abundance of fish smaller than 470 mm could only be estimated from tags recaptured at the Russian River weir, because no tagged fish in this size class were detected passing the Hidden Creek weir. Similarly, the abundance of fish greater than 569 mm could only be estimated from tags recaptured at the Russian River weir, because only 3 tagged fish in this size class were detected passing the Hidden Creek weir and this small sample was considered inadequate (Schwarz and Taylor 1998).

Our mark–recapture estimates of sockeye salmon abundance passing rkm 31.1 derived from tags recaptured at the 2 weir sites were not consistent. Tag recaptures were available from the 370–629 mm length strata at the Russian River weir allowing for an overall abundance estimate of 3,025,997 (95% CI = 2,464,629 to 3,586,366) sockeye salmon passing rkm 31.1 (Table 3). This abundance estimate was significantly (P<0.001) greater than the DIDSON abundance estimate of 1,715,963 for these length strata (Table 4). The Russian River weir estimates were significantly greater than the DIDSON estimates for the 2 smallest length strata (370–519) and the largest length stratum (570–629 mm), but the mark–recapture and DIDSON estimates were not different for the 520–569 length stratum. Tag recaptures were available from the 470–569 mm length strata at the Hidden Creek weir allowing for an abundance estimate of 547,910 (95% CI = 455,905 to 641,915) sockeye salmon passing rkm 31.1 (Table 3). This abundance estimate was significantly (P<0.001) less than the DIDSON abundance estimate of 1,010,829 for these size classes (Table 3). Using tag recaptures from the 470–569 mm length strata at both weirs resulted in an abundance estimate of 855,617 (95% CI = 751,097 to 960,138) sockeye salmon passing rkm 31.1 (Table 3), which was also significantly (P<0.001) less than the DIDSON abundance estimate for these length strata. The Russian River weir mark–recapture abundance estimate (470–569 mm) was also significantly (P<0.001) greater than (2.36 times) the Hidden Creek weir estimate (Table 4).

2007

In 2007, we were generally able to apply PIT tags in proportion to daily DIDSON estimates of sockeye salmon passage during July, but the number of tags applied in August was higher relative to the sonar passage estimates, apparently due to an increase in fish wheel catchability (Figure 4). As in 2006, sonar data indicated a shift in sockeye salmon distribution from offshore to more near shore later in the season causing the apparent increase in fish wheel catchability.

The crew scheduling changes implemented in 2007 resulted in an increase in the number of PIT tags applied. We applied PIT tags to 8,077 (310–690 mm) and radio tags to 234 (437–651 mm) sockeye salmon at rkm 31.1 between July 1 and August 23. Approximately the same number of PIT tags were applied on the north bank (4,022) and south (4,055) banks. Ninety-three percent of radio tagged sockeye salmon migrated past the fixed receiver at rkm 45.1, and 86% migrated upstream of Naptowne Rapids at rkm 63.7 (Table 2, Appendix A2). Estimated tagging-induced mortalities to rkm 45.1 (7%) and 63.7 (14%) were significantly (P<0.05) different. At the Hidden Creek weir, 16,491 (450–609 mm) sockeye salmon were scanned for tags, and 155 PIT tags were detected. At the Russian River weir, 55,379 (360–609 mm) sockeye salmon were scanned for tags, and 250 PIT tags were detected. As in 2006, the daily number of PIT tags detected passing through Hidden Creek and Russian River weirs increased relative to the number of fish scanned for tags later in August (Figure 5). The size frequency distributions of untagged sockeye salmon were estimated with samples collected at the Hidden Creek (n=1,103) and Russian River weirs (n=229). Since no tag loss was detected in 2006, we assumed no tag loss occurred in 2007. Daily tests indicated that tag detection was >95% on 100% and 96% of the days at Hidden Creek and Russian River weirs, respectively.

Initial capture probabilities (p1) decreased with fish length up to about 550 mm and then increased (Figure 7). Chi-square tests identified 5 length strata corresponding with changes in initial capture probabilities (Table 5). The same 4 length strata were used for the abundance estimates derived from tag recaptures at the 2 weir recapture sites. The abundance of fish smaller than 450 mm could only be estimated from tags recaptured at the Russian River weir, because no tagged fish in this size class were detected passing the Hidden Creek weir.

Our mark–recapture estimates of sockeye salmon abundance passing rkm 31.1 derived from tags recaptured at the 2 weir sites were consistent in 2007. Tag recaptures were available from the 360–610 mm length strata at the Russian River weir allowing for an overall abundance estimate of 1,286,624 (95% CI = 1,113,646 to 1,459,602) sockeye salmon passing rkm 31.1 (Table 5). This abundance estimate was not significantly (P=0.098) different from the DIDSON abundance estimate of 1,115,119 for these length strata (Table 5). Tag recaptures were available from the 450–610 mm length strata at the Hidden Creek weir allowing for an abundance estimate of 1,039,867 (95% CI = 655,731 to 1,424,002) sockeye salmon passing rkm 31.1 (Table 5). This abundance estimate was not significantly (P=0.763) different from the DIDSON abundance estimate of 1,096,990 for these size classes (Table 5). Using tag recaptures from the 450–610 mm length strata at both weirs resulted in an abundance estimate of 1,078,011 (95% CI = 940,879 to 1,215,143) sockeye salmon passing rkm 31.1 (Table 5), which also was not significantly (P<0.814) different from the DIDSON abundance estimate for these length strata. The Russian River weir mark–recapture abundance estimate (450–610 mm) was also not significantly (P<0.427) different from the Hidden Creek weir estimate (Table 4).

2008

In 2008, we adjusted our August tagging rate to match the July rate, resulting in a generally more consistent number of PIT tags applied relative to daily DIDSON estimates of sockeye salmon passage (Figure 4). As in 2006–2007, sonar data indicated a shift in sockeye salmon distribution from offshore to nearshore later in the season causing an apparent increase in fish wheel catchability, but our strategy of adjusting tagging rates relative to fish wheel catch largely corrected for these changes.

We applied PIT tags to 4,958 (320–660 mm) and radio tags to 232 (380–640 mm) sockeye salmon at rkm 31.1 between July 7 and August 17. Substantially more PIT tags were applied on the north bank (3,617) than on the south bank (1,341). Eight-nine percent of radio tagged sockeye salmon migrated past the fixed receiver at rkm 45.1, and 84% migrated upstream of Naptowne Rapids at rkm 63.7 (Table 2, Appendix A3). Estimated tagging-induced mortalities to rkm 45.1 (11%) and 63.7 (16%) were not significantly (P=0.204) different. At the Hidden Creek weir, 13,870 (450–569 mm) sockeye salmon were scanned for tags, and 110 PIT tags were detected. At the Russian River weir, 46,638 (370–669 mm) sockeye salmon were scanned for tags, and 222 PIT tags were detected. As in 2006–2007, the daily number of PIT tags detected passing through Hidden Creek and Russian River weirs increased relative to the number of fish scanned for tags later in August (Figure 5). The size frequency distributions of untagged sockeye salmon were estimated with samples collected at the Hidden Creek (n=642) and Russian River weirs (n=566). Since no tag loss was detected in 2006, we assumed no tag loss occurred in 2008. Daily tests indicated that tag detection was >95% on 98% and 100% of the days at Hidden Creek and Russian River weirs, respectively.

Initial capture probabilities (p1) were generally highest for fish 450–489 mm in (Figure 8, Table 6). Chi-square tests identified 4 length strata corresponding with changes in initial capture probabilities (Table 6). The same 2 length strata were used for the abundance estimates derived from tag recaptures at the 2 weir recapture sites. The abundance of fish smaller than 450 mm and greater than 569 mm could only be estimated from tags recaptured at the Russian River weir, because insufficient numbers of tags were detected at Hidden Creek weir for these length strata (Schwarz and Taylor 1998).

Our mark–recapture estimates of sockeye salmon abundance passing rkm 31.1 derived from tags recaptured at the 2 weir sites were somewhat consistent in 2008. Tag recaptures were available from the 370–669 mm length strata at the Russian River weir allowing for an overall abundance estimate of 1,039,495 (95% CI = 839,523 to 1,239,466) sockeye salmon passing rkm 31.1 (Table 6). This abundance estimate was not significantly (P=0.182) different from the DIDSON abundance estimate of 899,513 for these length strata (Table 6). Tag recaptures were available from the 450–569 mm length strata at the Hidden Creek weir allowing for an abundance estimate of 297,216 (95% CI = 224,093 to 334,339) sockeye salmon passing rkm 31.1 (Table 6). This abundance estimate was significantly (P<0.001) less than the DIDSON abundance estimate of 450,204 for these size classes (Table 6). Using tag recaptures from the 450–569 mm length strata at both weirs resulted in an abundance estimate of 304,453 (95% CI = 267,965 to 340,940) sockeye salmon passing rkm 31.1 (Table 6), which also was significantly (P<0.001) less than the DIDSON abundance estimate for these length strata. The Russian River weir mark–recapture abundance estimate (450–569 mm) was not significantly (P<0.301) different from the Hidden Creek weir estimate (Table 4), and both estimates for these length strata were significantly less than the DIDSON estimate. The overall Russian River mark–recapture and DIDSON estimates (370–669 mm) we not significantly different, because the mark–recapture estimates for the 370–449 mm and 570–669 mm strata were higher, whereas the mark–recapture estimates for the 450–569 mm strata were lower than the DIDSON estimates. Thus, when the mark–recapture and DIDSON estimates for all length strata were summed, the overall estimates were not different.

Pooling data from both weirs, our mark–recapture abundance estimates were significantly less than the DIDSON estimates in 2006 and 2008 but not in 2007 (Tables 3, 5, 6). A linear regression of the pooled mark–recapture estimates (dependent variable) against the DIDSON estimates (2006–2008) resulted in a slope (m=1.12, se=0.19) not significantly different from one (P=0.628) and an intercept (b= -208532, se=162522) not significantly different from zero (P=0.421). The regression was then run again with the intercept set at zero and this also resulted in a slope (m=0.90, se=0.07) not significantly different from one (P=0.269) indicating that the DIDSON and mark–recapture methods were measuring the same abundances (Figure 9).

SPAWNER MIGRATION AND DISTRIBUTION

2006

In 2006, mean migration time declined significantly during the season for radio tagged sockeye salmon swimming between fixed radiotelemetry stations located at rkm 31.1–45.1 and 80.5–104.6 (Table 7). Between the sonar site and recapture fish wheels (rkm 31.1–45.1), mean migration time declined from 3.1 to 1.2 days from early July to late August. Between the outlet and inlet of Skilak Lake (rkm 80.5–104.6), mean migration time declined from 16.0 to 3.5 days, but 2 fish tagged during the first release period migrated between these 2 stations in 1.2 days. Between these same 4 sites, mean migration speeds increased during the season, but the changes were only significant between rkm 31.1–45.1 and marginally significant between rkm 80.5–104.6 (Table 7). Between the sonar site and recapture fish wheels (rkm 31.1–45.1), mean migration speed increased from 4.7 to 14.0 km day^{-1}. Between the outlet and inlet of Skilak Lake (rkm 80.5–104.6), mean migration speed increased from 4.9 to 7.3 km day^{-1} during the season, but 2 fish tagged during the first release period migrated 22.2 km day^{-1}. The highest overall mean migration speed (10.8 km day^{-1}) was between rkm 45.1–80.5.

Radiotagged sockeye salmon later relocated in the upper Kenai River watershed exhibited the earliest run timing past rkm 31.1, but this group was a relatively minor component of the total run. The migration past rkm 31.1 peaked the week beginning July 15 for fish later relocated in the upper Kenai River and July 22 for fish later relocated in the Skilak outlet area (Figure 9). The migration past rkm 31.1 was bimodal for fish later relocated in the Kenai River mainstem and Skilak inlet areas. Comparison of weekly DIDSON abundance estimates and number of radio tags applied indicated disproportionate tagging during the week beginning July 22 and again in late August (Figure 10). The majority (73%) of sockeye salmon radiotagged at rkm 31.1 migrated to the Skilak outlet (Zone 4 – 20%), Skilak inlet (Zones 6, 11, 13 – 20%), Kenai River mainstem (Zones 15, 17 – 23%), and Upper Kenai tributary (Zones 14, 16, 18–24 – 11%) spawning areas (Table 8, Figure 11). Only 1% of radiotagged sockeye salmon migrated to the Hidden Creek drainage and 4% to the Russian River drainage.

2007

In 2007, mean migration time again declined significantly during the season for radiotagged sockeye salmon swimming between fixed radiotelemetry stations located at rkm 31.1–45.1 and 80.5–104.6 (Table 9). Between the sonar site and recapture fish wheels (rkm 31.1–45.1), mean migration time declined from 3.5 to 1.5 days from early July to mid-August. Between the outlet and inlet of Skilak Lake (rkm 80.5–104.6), mean migration time declined from 27.9 to 12.3 days, but 3 fish tagged during the first release period migrated between these 2 stations in 7.7 days. Mean migration speeds of fish swimming between rkm 31.1–45.1, rkm 80.5–104.6, and rkm 104.6–132.0 changed significantly during the season (Table 9), but there was no consistent temporal trend. The highest overall mean migration speed (12.9 km day^{-1}) was again between rkm 45.1–80.5.

Radiotagged sockeye salmon later relocated in the Kenai River mainstem and upper Kenai River tributaries exhibited the earliest run timing past rkm 31.1, with the peak of their migration occurring the week beginning July 22 (Figure 10). Fish migrating to the Skilak outlet and inlet spawning areas exhibited a more protracted timing past rkm 31.1, with the peak of their migration occurring between July 22–August 5 (Figure 10). Comparison of weekly DIDSON abundance estimates and number of radio tags applied indicated disproportionate tagging during the weeks beginning July 15 and 22 (Figure 10). The majority (65%) of sockeye salmon radiotagged at rkm 31.1 migrated to the Skilak outlet (Zone 4 – 10%), Skilak inlet (Zones 6, 11, 13 – 9%), Kenai River mainstem (Zones 15, 17 – 26%) and Upper Kenai tributary (Zones 14, 16, 18–24 – 21%) spawning areas (Table 8; Figure 12). Only 1 radiotagged sockeye salmon (<1%) migrated to the Hidden Creek drainage, and 3% of radiotagged sockeye salmon migrated to the Russian River drainage.

2008

In 2008, mean migration time changed significantly during the season for radiotagged sockeye salmon swimming between fixed radiotelemetry stations located at rkm 31.1–45.1 (Table 10), but there was no consistent temporal trend. Mean migration speeds between the fixed stations did not change significantly during the season (Table 10), and the highest overall mean migration speed (10.5 km day^{-1}) was again between rkm 45.1–80.5.

Radiotagged sockeye salmon later relocated in the Skilak inlet, Kenai River mainstem, and upper Kenai River tributaries exhibited the earliest run timing past rkm 31.1, with the peak of their migration occurring the week beginning July 15 (Figure 10). Fish migrating to the Skilak inlet Kenai River mainstem spawning areas exhibited a secondary timing peak at rkm 31.1 during the week beginning July 29 (Figure 10). The migration to the Skilak outlet spawning area peaked during the week beginning July 22 (Figure 10). Comparison of weekly DIDSON abundance estimates and number of radio tags applied indicated disproportionate tagging during the week beginning July 29 (Figure 9). The majority (59%) of sockeye salmon radiotagged at rkm 31.1 migrated to the Skilak outlet (Zone 4 – 10%), Skilak inlet (Zones 6, 11, 13 – 16%), Kenai River mainstem (Zones 15, 17 – 22%), and Upper Kenai tributary (Zones 14, 16, 18–24 – 11%) spawning areas (Table 8, Figure 13). Only 4% of radiotagged sockeye salmon migrated to the Hidden Creek drainage and 3% to the Russian River drainage.

Mean migration speeds of all subpopulations combined between rkms 31.1–45.1 were significantly higher (P<0.001) in 2006 (9.9 km day^{-1}, SE=0.4) and 2007 (10.8 km day^{-1}, SE=0.4) than in 2008 (8.1 km day^{-1}, SE=0.4). Mean annual migration speeds were not significantly correlated (P>0.10) with mean date of migration past rkm 31.1, but run timing was later than average in 2006 (10 days late) and 2007 (4 days late) compared with 2008 (on time).

DISCUSSION

ABUNDANCE

Uncertainty in our mark–recapture abundance estimates precluded a definitive conclusion regarding the accuracy of the DIDSON estimate in 2006. Our mark–recapture abundance estimates derived from the rkm 45.1 fish wheels were likely biased high due to poor tag detection. Our Russian River mark–recapture estimate was significantly greater than the DIDSON estimate, while the Hidden Creek estimate was significantly less than the DIDSON estimate. In addition, the Russian River estimate was significantly greater than the Hidden Creek estimate. In 2007, the Russian River and Hidden Creek mark–recapture abundance estimates were not significantly different from the DIDSON estimates, and they were not significantly different from each other. In 2008, the Russian River and Hidden Creek mark–recapture abundance estimates were not significantly different from each other, but the Hidden Creek estimate was significantly less than the DIDSON estimate. Our mark–recapture abundance estimates derived from the weirs may have been biased due primarily to violations of assumptions 1 and 2. Below we discuss the validity of these estimates organized by the assumptions upon which they were predicated.

Assumption 1: Closed population (i.e., no mortality or recruitment).

Greater tagging-induced mortality for fish migrating to the Russian River weir could account for the consistently higher abundance estimates obtained from recoveries at this site (Tables 3–6). We attempted to correct our abundance estimates for tagging-induced mortality by reducing the number of PIT tags released (and available for recapture) using estimates of survival of radiotagged fish. Our estimates of tagging-induced mortality approximately doubled between rkm 45.1 and 63.7 (Table 2), leading us to question whether our survival estimate from rkm 63.7

adequately corrected for all tagging-induced mortality as the fish migrated farther from the tagging site to weirs located at rkm 108.4 (Hidden Creek) and 125.9 (Russian River). Underwood et al. (2004) and Bromaghin et al. (2007) concluded that tagging-induced mortality accounted for a decline in marked fractions of chum salmon *Oncorhynchus keta* captured in fish wheels at greater distances from the tagging site. Although, we were not able to directly estimate tagging-induced mortality of radiotagged fish as they migrated upstream of rkm 63.7 (due to spawning activity), we can estimate the survival of tagged fish reaching Hidden Creek (80%) and Russian River (76%) weirs assuming mortality of tagged fish increased linearly (i.e., approximately 0.2% km^{-1}) away from the tagging site. These estimates indicate the probable magnitude of the difference in tagging-induced mortality between the 2 stocks, but they were not used in the abundance estimates.

Inriver fishing mortality differences are another source of error that could account for the higher Russian River abundance estimates. Inriver fisheries ensured that populations were not closed in our experiments. But, so long as tagged and untagged fish were harvested at the same rate, our abundance estimates would not be biased. However, Bromaghin et al. (2007) and Yanusz et al. (2007) found that radiotagged chum and sockeye salmon probably migrated more slowly than untagged salmon in the Yukon and Susitna rivers. If so, tagged fish would be exposed to inriver fisheries for a longer time leading to a higher harvest rate compared to untagged fish. Differences in fishing mortalities between tagged and untagged fish would be greatest for fish migrating through the intense Russian River fishery.

Other investigators have documented levels of mortality among radiotagged sockeye salmon similar to those obtained in this study. Cooke et al. (2006) estimated 9.7% of radiotagged sockeye salmon did not migrate upstream of Hell’s Gate on the Fraser River, and 14.2% of those that successfully passed Hell’s Gate were not detected entering natal spawning grounds. Although, we were not able to estimate tagging-induced mortality above Naptowne Rapids (rkm 63.7), it is likely that tagged fish migrating to Russian River weir may have suffered higher mortality than fish migrating to Hidden Creek weir, because they had to pass through the Kenai River canyon and the Russian River falls.

Tagging-induced mortality is likely caused by stress-related physiological changes induced by hyperactivity during capture. Laboratory studies have shown that the stress of capture causes blood lactic acid levels to increase for up to 4 hours after capture with mortality occurring if critical levels of lactate are reached (Parker and Black 1959; Parker et al. 1959; Farrell et al. 2000). Candy et al. (1996) documented an increase in delayed mortality (8–12 hours after release) of sonic-tagged Chinook salmon held less than 15 mins (0%) versus greater than 30 mins (50%). In our study, we found no difference between radiotagged survivors and non-survivors (P=0.60) in the amount of time lapsed between checks of the fish wheel live boxes. However, the elapsed time between checks of the live box was not the actual holding time of individual fish, because we did not know when each individual fish entered the box.

Assumption 2: Either the probability of capture was constant across all individuals at the time of capture (constant p_1), or marked fish mixed uniformly with unmarked fish before the recapture event, or the probability of capture was constant across all individuals at the time of recapture (constant p_2).

Because salmon entering the river at the beginning of the run did not mix with those entering at the end of the run before reaching the weirs, the *marked fish* were not *mixed uniformly with* *unmarked fish before the recapture event.* Also, the *probability of capture was* not *constant across all individuals at the time of recapture*, because fish migrating to the 2 weirs had a 100% probability of capture while those migrating to other parts of the drainage had a 0% probability of capture. Therefore, to meet assumption 2, we needed to ensure that the *probability of capture was constant across all individuals at the time of capture.* We stratified by size in an attempt to correct for size-dependent fish wheel capture probabilities (Figures 6–8). If this scheme were successful, abundance estimates derived from the 2 weir recapture sites should not have differed within size strata. But, it appeared that capture probabilities also changed over time due to tagging rate changes during the run (Figure 4). However, temporal stratification was not possible due to apparent differences in migration rates of tagged and untagged fish (Figure 5). Therefore, different abundance estimates between weir sites in 2006 (Table 4) could have resulted from temporal changes in capture probabilities and differences in run timing between the 2 stocks at the rkm 31.1 tagging site. More uniform temporal tagging rates in 2007 and 2008 may account for lack of any significant differences between abundance estimates from the 2 weir sites in those years.

Assumption 3: Marking did not affect catchability

All fish were enumerated and checked for marks at the weirs causing the probability of capture at each weir to be 100%. Thus, catchability for fish returning to weirs could only have been affected by the tagging process if movement probabilities were altered where tagged fish were less likely to reach the weirs than untagged fish. Because tagging-induced mortality increased with distance from the tagging site (Table 2), it is reasonable to conclude that some tagged fish may not have reached the weirs (a sublethal tagging effect). The magnitude of this source of error is unknown, but future analyses of genetic data may provide for an estimate of stock-origin for individual tagged fish allowing us to further investigate it.

Assumption 4: *Tags were not lost.*

Of the 89 adipose-clipped fish that were recaptured at the rkm 45.1 fish wheel, no PIT tag loss was detected. Based on this sample size and finding zero loss, we can be 95% confident that PIT tag loss was no greater than 3.4%. Thus, we did not apply tag loss corrections for any estimate.

Assumption 5: *All tags were recognized and reported.*

Daily tag detection tests conducted in 2006 with PIT tags in neutrally buoyant vials resulted in detection rates >95% on 89% and 96% of the days at Hidden Creek and Russian River weirs, respectively. But, subsequent tag detection tests conducted with live fish tagged at the weirs suggested that detection rates estimated with the vials were biased high. However, we recognized that the behavior of fish tagged at the weirs was different than that of fish tagged at rkm 31.1, because recent handling caused these fish to swim through the antennas differently than other fish passing through during normal operations. These results led us to install redundant PIT tag antennas at both weirs in 2007, which provided for estimates of tag detection rates for fish tagged at rkm 31.1 with the assumption that the detection rates of the 2 antennas at each weir were independent of each other. The antennas operated in 2007 (attached directly to the live box) were found to have tag detection rates >95% on 100% and 96% of the days at Hidden Creek and Russian River weirs, respectively. These results suggested that the single antennas operated in 2006 (also attached directly to the live box) probably also provided high detection rates. But, since redundant antennas were not operated in 2006, we cannot be certain that the 2007 tag detection results apply directly to the 2006 antennas.

SPAWNER MIGRATION AND DISTRIBUTION

In the present study, average sockeye salmon migration speeds were 5–14 km day^{-1} and more than doubled from early July to mid-August below rkm 45.1 (Tables 7–9). In a previous tagging study, Tarbox (1988) estimated the maximum migration speed of sockeye salmon in rivers was about 20 km day^{-1}. Using run reconstruction, Mundy et al. (1993) estimated that residence time of Kenai River sockeye salmon in Cook Inlet declined by a factor of 3 during July, suggesting an increase in migration speed during the run. Yanusz et al. (2007) observed an increase in migration speed (2.0–13.5 km day^{-1}) of sockeye salmon during the run for fish tagged at Flathorn in the Susitna River. Higher migration speeds later in the run likely result because individuals entering the river late tend to be more reproductively advanced. Yanusz et al. (2007) also concluded that the migration speeds of radiotagged sockeye salmon were likely slower than untagged fish. If so, our migration speed estimates may be biased low.

We found that the run timing of fish spawning in upper Kenai River tributaries was relatively early in each year of the study (Figure 9). A similar pattern has been observed in other sockeye salmon populations with upper tributary spawners migrating and spawning earlier in the run (Hartman et al. 1963; Narver 1968; Nelson 1983; Owen et al. 1962). These studies have also shown that lakeshore and outlet spawning subpopulations tended to exhibit later run timing. We found that the run timing of the Skilak outlet subpopulation was relatively late in 2007–2008 but not in 2006 (Figure 9). The numbers of fish apparently spawning in Skilak Lake was too small to estimate run timing. Finally, the mean annual migration speed of all subpopulations combined was weakly associated with run timing past rkm 31.1 suggesting that fish migrated upstream faster when run timing was later than average.

The distribution of sockeye salmon spawners within the Kenai River watershed in part determines the mechanisms regulating salmon production in this system. We found that about 35–42% of the run likely spawned within the mainstem Kenai River above Skilak Lake (Table 8). This subpopulation likely experienced a relatively stable physical environment compared to smaller upper tributary streams subjected to greater fluctuations in water level and temperature. However, having the majority of spawners concentrated within about a 50 km stream segment may also contribute to greater fluctuations in survival for the stock as a whole, because a large fraction of the stock probably experiences similar embryo-spring fry survivals. Perhaps these characteristics contribute to the relatively high variability in returns per spawner (1.9 to 15.8) observed in this system (Edmundson et al. 2003). The fry produced by these spawners likely all rear in Skilak Lake, which is consistent with our previous estimates of the importance of this lake for salmon production in the watershed (DeCino et al. 2004; Edmundson et al. 2003). We found that about 10–20% of the run likely spawned within the mainstem Kenai River at the outlet of Skilak Lake (Table 8). Emergent fry produced by this outlet subpopulation migrate upstream to rear in Skilak Lake. Emergent fry migrating upstream are probably more dependent on yolk energy reserves and spring food resources to successfully complete their migration (McCart 1967). If so, the outlet spawning subpopulation may be more likely to exhibit the brood interaction described by Edmundson et al. (2003), and interannual changes in the abundance of this subpopulation may determine whether this mechanism significantly affects the population dynamics of the stock as a whole.

CONCLUSIONS

Overall, our mark–recapture abundance estimates did not support the conclusion that the DIDSON estimates were consistently biased during the 3 years of this study. In 2006, the Russian mark–recapture estimate was significantly higher while the Hidden mark–recapture estimate was significantly lower than the DIDSON estimate. The Russian and Hidden mark–recapture estimates were also significantly different from each other in 2006. Variable tagging-induced mortality or initial capture probabilities between the 2 stocks were likely causes of these observed differences. The Russian and Hidden mark–recapture estimates were not significantly different from each other in 2007–2008, and in 2007 the mark–recapture estimates from both weirs were not significantly different from the DIDSON estimate. However in 2008, the Russian mark–recapture estimate was not significantly different while the Hidden mark–recapture estimate was significantly lower than the DIDSON estimate. The differences between these estimates were due to the different length strata included in the Russian and Hidden mark–recapture estimates. A linear regression of the pooled mark–recapture estimates (dependent variable) against the DIDSON estimates (2006–2008) resulted in an intercept not significantly different from zero and a slope not significantly different from one indicating that the DIDSON and mark–recapture methods were measuring the same abundances.

Radiotelemetry studies indicated that 35–42% of sockeye salmon spawned in the mainstem Kenai River between the Russian River confluence and Skilak Lake. Another 10–20% spawned in an approximately 16 km segment of the Kenai River immediately below Skilak Lake, while 11–21% spawned in upper tributaries of the watershed (Russian River, Quartz Creek, Trail Lakes, Ptarmigan Creek, etc). Finally, 7–11% spawned in Skilak Lake and its tributaries (i.e. King County Creek, Hidden Creek, and Skilak River), and 19–31% either did not migrate above Naptowne Rapids or were caught in sport or personal use fisheries or were not relocated after initial release. Sockeye salmon migrating to the upper tributaries exhibited slightly earlier run timing past the rkm 31.1 sonar site, while those migrating to the mainstem Kenai River above Skilak Lake exhibited later run timing.

ACKNOWLEDGMENTS

This project was conducted cooperatively by the ADF&G Divisions of Commercial Fisheries and Sport Fish, and the Cook Inlet Aquaculture Association. From ADF&G Division of Commercial Fisheries: L. Fair, D. Westerman, T. Tobias, C. Habicht, and J. Berger contributed to the design and implementation of the study. T. Tobias interpreted scale ages and tracked genetic samples. K. Rudge-Karic supervised the tagging crew, conducted field logistics, entered data, and assisted with construction of the project database. From ADF&G Division of Sport Fish: B. Clark, J. Hasbrouck, R. Massengill, P. Berkhahn, and M. Hatfield contributed to the design and implementation of the study.

The following seasonal staff at remote field camps provided very long days, dedication, and patience collecting the data. From the Division of Commercial Fisheries, R. Wilcox, N. Bittle, P. Ischi, J. Kell, C. Nicks, N. King, T. Boyd, D. Tayor, and M. Mazurek contributed. From the Division of Sport Fish, T. Johnson, J. Cope, J. Strait, K. Strausbaugh, and S. Simons contributed.

From CIAA, G. Frandrei, and T. Dodson provided logistics and supervision. Technical assistance with computer programming was provided by R. Murray. J. Carlon constructed a radiotelemetry database. J. DeCreeft (Northwind Aviation) assisted with aerial radiotelemetry surveys.

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TABLES AND FIGURES

Table 1.–Possible states of fish at the recapture fish wheels (rkm 45.1) and action taken.

Adipose missing	PIT tag present	PIT tag decoded	Radio Tag Present	Never Tagged	Data Recorded	Action
X	X	X			Record PIT tag no.	Release
X	X				PIT tag malfunction	MEFL, Sacrifice
X					PIT tag loss	MEFL, Sacrifice
X	X	X	X		Record PIT tag no.	Release
X	X		X		PIT tag malfunction	MEFL, Sacrifice, Reuse radio tag
X			X		PIT tag loss	MEFL, Sacrifice, Reuse radio tag
X	X	X			Radio tag loss	Record PIT tag #, Release.
				X	Totals by hour	MEFL every 15th, Release

Table 2.–Number of radio tags applied at rkm 31.1, number of radiotagged fish caught in personal use and sport fisheries, and estimated fraction of radiotagged sockeye salmon surviving tagging effects and migrating past rkms 45.1 and 63.7, 2006–2008.

Year	Zone (Range rkm)	Number Tagged	No. Caught in Zone	Number Not Caught	Number Not Migrating Upstream	Number with Mortality Codes	Estimated Survival	Estimated Mortality
2006	31.1–45.1	215	8	207	11	6	0.95	0.05
	31.1–63.7	215	11	204	23	11	0.89	0.11
2007	31.1–45.1	234	21	213	14	10	0.93	0.07
	31.1–63.7	234	27	207	30	18	0.86	0.14
2008	31.1–45.1	232	26	206	22	16	0.89	0.11
	31.1–63.7	232	34	198	32	22	0.84	0.16

Table 3.–Comparison of mark–recapture and DIDSON estimates of sockeye salmon abundance passing rkm 31.1 from July 1 to August 24, 2006.

Length Stratum (mm)	M-R Estimate	V(n)	95% Confidence Interval Lower	95% Confidence Interval Upper	n1	n2	m2	p_1	p_2	DIDSON sonar Estimate	V(n)	*Z-test* *P*-value	Ratio
Russian River weir as recovery site													
370–469	273,701	4.1E+09	148,195	399,207	232	18,809	15	0.001	0.065	65,215	1.1E+07	0.001	4.20
470–519	423,337	4.8E+09	287,205	559,470	600	23,939	33	0.001	0.055	168,860	7.1E+07	0.000	2.51
520–569	869,684	9.3E+09	680,744	1,058,624	2993	22,657	77	0.003	0.026	841,969	1.8E+09	0.776	1.03
570–629	1,459,275	6.4E+10	965,280	1,953,270	2275	20,519	31	0.002	0.014	639,920	1.0E+09	0.001	2.28
Total	3,025,997	8.2E+10	2,465,629	3,586,366	6,100	85,924	156	0.002	0.026	1,715,963	2.9E+09	0.000	1.76
Hidden Creek weir as recovery site													
470–519	138,437	1.4E+08	115,586	161,288	600	26,018	112	0.004	0.187	168,860	7.1E+07	0.034	0.82
520–569	409,473	2.2E+09	318,288	500,658	2993	10,120	73	0.007	0.024	841,969	1.8E+09	0.000	0.49
Total	547,910	2.3E+09	453,905	641,915	3,593	36,138	185	0.005	0.051	1,010,829	1.8E+09	0.000	0.54
Russian and Hidden weirs combined													
470–519	205,728	2.2E+08	176,831	234,625	600	49,957	145	0.003	0.242	168,860	7.1E+07	0.029	1.22
520–569	649,890	2.6E+09	549,444	750,336	2993	32,777	150	0.005	0.050	841,969	1.8E+09	0.004	0.77
Total	855,617	2.8E+09	751,097	960,138	3,593	82,734	295	0.004	0.082	1,010,829	1.8E+09	0.023	0.85
rkm 45.3 fish wheel as recovery site													
370–539	2,196,284	5.7E+11	722,458	3,670,110	1,673	18,574	22	0.001	0.013	470,654	5.5E+08	0.021	4.67
540–589	2,323,605	1.6E+11	1,535,909	3,111,301	3,789	27,971	57	0.002	0.015	1,065,935	2.8E+09	0.002	2.18
590–699	1,072,517	9.5E+10	469,644	1,675,389	902	13,064	10	0.001	0.011	253,754	1.6E+08	0.008	4.23
Total	5,592,406	8.2E+11	3,815,869	7,368,943	6,365	59,609	89	0.001	0.014	1,790,344	3.6E+09	0.000	3.12

Table 4.–Comparison of mark–recapture estimates of sockeye salmon abundance passing rkm 31.1 based upon tag recaptures at the Russian River and Hidden Creek weirs, 2006–2008.

	Length	Russian River		Hidden Creek			
Year	stratum (mm)	Estimate	V(n)	Estimate	V(n)	Z-test P	Ratio
2006	470–569	1,293,021	1.4E+10	547,910	2.3E+09	0.000	2.36
2007	450–609	0	0.0E+00	1,039,867	3.8E+10	0.000	1.16
2008	450–569	0	0.0E+00	279,216	7.9E+08	0.000	1.64

Table 5.–Comparison of mark–recapture and DIDSON estimates of sockeye salmon abundance passing rkm 31.1 from July 1 to August 23, 2007.

Length	M-R		95% Confidence Interval							DIDSON sonar		*Z-test*	
Stratum (mm)	Estimate	V(n)	Lower	Upper	n1	n2	m2	p_1	p_2	Estimate	V(n)	*P*-value	Ratio
			Russian River weir as recovery site										
360–449	80,326	5.9E+08	32,647	128,004	109	6,558	8	0.001	0.073	18,129	8.2E+05	0.010	4.43
450–489	26,873	2.0E+07	18,157	35,588	206	3,886	29	0.007	0.141	34,259	2.9E+06	0.119	0.78
490–549	596,974	3.1E+09	488,591	705,358	2,060	31,576	108	0.003	0.052	341,873	2.9E+08	0.000	1.75
550–579	225,661	6.7E+08	174,916	276,407	2,571	6,315	71	0.011	0.028	426,806	4.6E+08	0.000	0.53
580–609	356,790	3.4E+09	241,681	471,898	1,772	7,044	34	0.005	0.019	294,053	2.2E+08	0.294	1.21
Total	1,286,624	7.8E+09	1,113,646	1,459,602	6,718	55,379	250	0.005	0.037	1,115,119	3.1E+09	0.098	1.15
			Hidden Creek weir as recovery site										
450–489	7,396	1.7E+06	4,823	9,968	206	926	25	0.027	0.121	34,259	2.9E+06	0.000	0.22
490–549	211,937	4.1E+08	172,023	251,852	2,060	10,387	100	0.010	0.049	341,873	2.9E+08	0.000	0.62
550–579	373,355	4.9E+09	236,265	510,446	2,571	3,918	26	0.007	0.010	426,806	4.6E+08	0.456	0.87
580–609	447,178	3.3E+10	90,574	803,782	1,772	1,260	4	0.003	0.002	294,053	2.2E+08	0.394	1.52
Total	1,039,867	3.8E+10	655,731	1,424,002	6,609	16,491	155	0.009	0.023	1,096,990	3.0E+09	0.763	0.95
			Russian and Hidden weirs combined										
450–489	18,150	4.3E+06	14,098	22,202	206	4,813	54	0.011	0.262	34,259	2.9E+06	0.000	0.53
490–549	413,750	7.3E+08	360,835	466,665	2,060	41,962	208	0.005	0.101	341,873	2.9E+08	0.024	1.21
550–579	268,629	6.9E+08	216,979	320,279	2,571	10,233	97	0.009	0.038	426,806	4.6E+08	0.000	0.63
580–609	377,481	3.5E+09	262,064	492,898	1,772	8,304	38	0.005	0.021	294,053	2.2E+08	0.166	1.28
Total	1,078,011	4.9E+09	940,879	1,215,143	6,609	65,312	397	0.006	0.060	1,096,990	3.0E+09	0.814	0.98

Table 6.–Comparison of mark–recapture and DIDSON estimates of sockeye salmon abundance passing rkm 31.1 from July 7 to August 17, 2008.

Length	M-R		95% Confidence Interval							DIDSON sonar		*Z-test*	
stratum (mm)	Estimate	V(n)	Lower	Upper	n1	n2	m2	p_1	p_2	Estimate	V(n)	*P*-value	Ratio
Russian River weir as recovery site													
370–449	159,221	1.2E+09	92,070	226,373	261	11,536	18	0.002	0.069	57,087	8.1E+06	0.003	2.79
450–489	12,410	3.0E+06	9,012	15,808	214	2,307	39	0.017	0.182	46,789	5.5E+06	0.000	0.27
490–569	305,543	6.5E+08	255,657	355,430	1,846	21,836	131	0.006	0.071	403,415	4.1E+08	0.003	0.76
570–669	562,320	8.6E+09	380,718	743,921	1,795	10,959	34	0.003	0.019	392,222	3.8E+08	0.071	1.43
Total	1,039,495	1.0E+10	839,523	1,239,466	4,116	46,638	222	0.005	0.054	899,513	8.1E+08	0.182	1.16
Hidden Creek weir as recovery site													
450–489	13,850	5.7E+06	9,185	18,515	214	1,802	27	0.015	0.126	46,789	5.5E+06	0.000	0.30
490–569	265,366	7.9E+08	210,441	320,291	1,846	12,068	83	0.007	0.045	403,415	4.1E+08	0.000	0.66
Total	279,216	7.9E+08	224,093	334,339	2,060	13,870	110	0.008	0.053	450,204	4.1E+08	0.000	0.62
Russian and Hidden weirs combined													
450–489	13,194	1.7E+06	10,613	15,775	214	4,109	66	0.016	0.308	46,789	5.5E+06	0.000	0.28
490–569	291,259	3.4E+08	254,863	327,655	1,846	33,904	214	0.006	0.116	403,415	4.1E+08	0.000	0.72
Total	304,453	3.5E+08	267,965	340,940	2,060	38,013	280	0.007	0.136	450,204	4.1E+08	0.000	0.68

Table 7.–Mean migration time (days) and speed (km day^{-1}) of radiotagged sockeye salmon between 4 fixed radiotelemetry stations on the mainstem Kenai River, 2006.

	rkm 31.1-45.1			rkm 45.1-80.5			rkm 80.5-104.6			rkm 104.6-132.0		
Week	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
							Migration Time (days)					
7/01–7/7	-	-	-	-	-	-	-	-	-	-	-	-
7/08–7/14	3.1	0.7	7	3.8	2.1	3	1.2	6.7	2	-	-	-
7/15–7/21	1.8	0.4	17	3.0	1.0	13	11.9	2.9	11	5.9	5.2	5
7/22–7/28	2.5	0.2	73	4.1	0.5	62	16.0	1.5	42	12.4	4.4	7
7/29–8/04	2.0	0.3	41	5.9	0.6	38	13.3	1.8	27	10.8	8.3	2
8/05–8/11	2.0	0.4	18	5.8	0.9	15	8.9	3.0	10	4.0	11.7	1
8/12–8/18	1.2	0.3	32	4.0	0.7	23	6.0	2.2	19	6.3	4.8	6
8/19–8/25	1.2	0.9	4	3.2	2.1	3	3.5	5.5	3	-	-	-
Mean	2.1	0.1	192	4.6	0.3	157	12.1	0.9	114	8.6	2.4	21
P-value	0.025			0.067			0.003			0.829		
							Migration Speed (km day^{-1})					
7/01–7/7	-	-	-	-	-	-	-	-	-	-	-	-
7/08–7/14	4.7	1.7	7	10.3	3.5	3	22.2	4.9	2	-	-	-
7/15–7/21	9.5	1.1	17	13.9	1.7	13	7.1	2.1	11	5.4	2.2	5
7/22–7/28	8.2	0.5	73	11.2	0.8	62	4.9	1.1	42	5.4	1.8	7
7/29–8/04	8.8	0.7	41	10.1	1.0	38	5.7	1.3	27	2.9	3.4	2
8/05–8/11	7.3	1.1	18	8.5	1.6	15	6.5	2.2	10	7.1	4.8	1
8/12–8/18	14.0	0.8	32	10.5	1.3	23	5.7	1.6	19	9.7	2.0	6
8/19–8/25	13.4	2.2	4	12.6	3.5	3	7.3	4.0	3	-	-	-
Mean	9.3	0.4	192	10.8	0.5	157	5.9	0.7	114	6.1	0.9	21
P-value	<0.001			0.358			0.062			0.389		

Table 8.–Final destinations of radiotagged sockeye salmon in the Kenai River watershed, 2006–2008.

		River Kilometer		2006		2007		2008	
Zone	Description	Begin	End	No. Tags	Proportion	No. Tags	Proportion	No. Tags	Proportion
1	Kenai River Mouth	0.0	31.1	4	0.02	4	0.02	7	0.03
2	Sonar Site to SF Fish Wheels	31.1	45.1	7	0.03	10	0.04	15	0.06
3	SF Fish Wheels to Upper Naptowne Rapids	45.1	63.7	12	0.06	16	0.07	10	0.04
4	Upper Naptowne Rapids to Skilak Outlet	63.7	80.5	44	0.20	23	0.10	23	0.10
5	Skilak Lake	80.5	104.6	11	0.05	14	0.06	16	0.07
6	Skilak Lake Inlet Staging Area	103.6	104.6	1	0.00	0	0.00	0	0.00
7	King County Creek Staging Area	87.9	87.9	1	0.00	1	0.00	0	0.00
8	King County Creek	87.9	87.9	0	0.00	0	0.00	0	0.00
9	Skilak River Staging Area	104.0	104.0	1	0.00	0	0.00	0	0.00
10	Skilak River	104.6	104.6	2	0.01	0	0.00	0	0.00
11	Skilak Lake Inlet to Boomerang Lake	104.6	106.5	38	0.18	17	0.07	33	0.14
12	Hidden Creek Drainage	104.6	104.6	2	0.01	1	0.00	9	0.04
13	Boomerang Lake to Jean Creek Slough	106.5	111.4	3	0.01	3	0.01	3	0.01
14	Jean Creek Drainage	111.5	111.5	0	0.00	1	0.00	2	0.01
15	Jean Creek to Russian River	111.4	118.9	37	0.17	39	0.17	37	0.16
16	Russian River Drainage	118.9	118.9	8	0.04	8	0.03	7	0.03
17	Russian River to Kenai Lake Outlet	118.9	132.0	12	0.06	22	0.09	14	0.06
18	Kenai Lake	132.0	167.7	0	0.00	2	0.01	2	0.01
19	Quartz Creek	136.5	136.5	9	0.04	32	0.14	4	0.02
20	Trail River-Ptarmagin Creek Staging Area	160.9	160.9	0	0.00	0	0.00	0	0.00
21	Trail River-Ptarmagin Creek	160.9	160.9	5	0.02	2	0.01	11	0.05
22	Snow River Staging Area	167.7	167.7	0	0.00	0	0.00	0	0.00
23	Snow River	167.7	167.7	0	0.00	2	0.01	0	0.00
24	Quartz Creek Staging Area	136.5	136.5	1	0.00	2	0.01	0	0.00
	Sport Caught			13	0.06	33	0.14	39	0.17
	Dip Net Caught			2	0.01	0	0.00	0	0.00
	Returned (unknown)			2	0.01	2	0.01	0	0.00
	Total			215	1.00	234	1.00	232	1.00

Table 9.–Mean migration time (days) and speed (km day^{-1}) of radiotagged sockeye salmon between 4 fixed radiotelemetry stations on the mainstem Kenai River, 2007.

	rkm 31.1-45.1			rkm 45.1-80.5			rkm 80.5-104.6			rkm 104.6-132.0		
Week	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
						Migration Time (days)						
7/01–7/7	3.5	2.9	8	3.5	1.9	4	7.7	6.1	3	16.3	18.1	3
7/08–7/14	2.9	3.1	17	9.0	-	1	40.0	-	1	13.1	4.5	8
7/15–7/21	1.7	1.2	47	6.5	13.2	30	21.4	16.9	17	10.6	6.1	17
7/22–7/28	2.9	2.1	42	5.7	11.8	32	27.9	15.6	21	20.0	12.8	7
7/29–8/04	3.0	3.8	13	8.3	8.9	12	12.5	12.4	18	3.0	0.0	2
8/05–8/11	1.7	0.7	20	7.3	10.5	19	12.9	15.6	22	6.7	9.5	6
8/12–8/18	1.5	0.8	13	7.6	14.1	10	12.3	12.2	8	10.5	4.9	2
8/19–8/25	2.0	0.0	3	4.5	2.1	2	17.0	-	1	-	-	-
Mean	2.3	0.2	163	6.6	1.1	110	18.0	1.7	91	12.0	1.4	45
P-value	0.019			0.994			0.010			0.096		
						Migration Speed (km day^{-1})						
7/01–7/7	5.6	4.3	7	12.2	5.9	4	9.9	13.1	3	4.0	4.1	3
7/08–7/14	8.0	4.3	17	3.8	-	1	0.6	-	1	2.2	0.8	8
7/15–7/21	10.4	4.2	46	14.8	9.5	30	2.7	2.5	17	3.5	2.2	17
7/22–7/28	6.9	4.1	42	12.3	7.9	30	2.1	3.1	21	1.8	1.3	7
7/29–8/04	8.3	4.4	13	10.6	12.2	11	6.9	7.9	18	8.5	0.0	2
8/05–8/11	9.9	3.8	20	13.0	9.8	19	7.4	7.2	22	8.3	4.4	6
8/12–8/18	10.9	4.1	13	13.9	9.3	10	6.5	8.0	8	2.7	1.3	2
8/19–8/25	7.0	0.0	3	8.6	4.1	2	1.5	-	1	-	-	-
Mean	8.8	0.3	161	12.9	0.9	107	5.1	0.7	91	3.9	0.5	45
P-value	0.001			0.820			0.052			0.001		

Table 10.–Mean migration time (days) and speed (km day^{-1}) of radiotagged sockeye salmon between 4 fixed radiotelemetry stations on the mainstem Kenai River, 2008.

	rkm 31.1-45.1			rkm 45.1-80.5			rkm 80.5-104.6			rkm 104.6-132.0		
Week	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
							Migration Time (days)					
7/01-7/7	-	-	-	-	-	-	-	-	-	-	-	-
7/08-7/14	2.0		1									
7/15-7/21	3.1	2.1	41	7.4	7.7	37	13.4	11.2	31	6.8	4.8	13
7/22-7/28	2.8	1.4	17	4.9	3.2	14	12.1	9.9	8	7.0	4.5	4
7/29-8/04	2.2	1.3	72	5.2	4.2	62	13.7	11.1	50	8.0	4.7	9
8/05-8/11	2.9	1.4	22	7.2	6.9	21	11.2	4.5	13	11.0	2.8	2
8/12-8/18	2.2	1.2	27	4.1	3.0	23	6.1	3.5	15	6.0		1
8/19-8/25												
Mean	2.5	0.1	180	5.8	0.4	157	12.2	0.9	117	7.5	0.8	29
P-value	0.020			0.090			0.119			0.805		
							Migration Speed (km day^{-1})					
7/01-7/7	-	-	-	-	-	-	-	-	-	-	-	-
7/08-7/14	7.0		1									
7/15-7/21	6.0	3.6	41	10.4	9.0	37	4.2	5.0	30	5.5	3.6	13
7/22-7/28	6.9	4.3	17	10.5	7.9	14	5.0	4.6	8	5.4	4.6	4
7/29-8/04	8.2	4.2	69	10.5	7.5	62	4.4	4.8	50	4.5	2.9	9
8/05-8/11	6.2	3.5	22	8.7	7.5	21	3.4	3.2	13	2.3	0.6	2
8/12-8/18	7.8	4.0	26	12.6	8.4	23	6.2	4.0	15	4.1		1
8/19-8/25												
Mean	7.3	0.3	176	10.5	0.6	157	4.5	0.4	116	4.9	0.6	29
P-value	0.068			0.624			0.562			0.763		

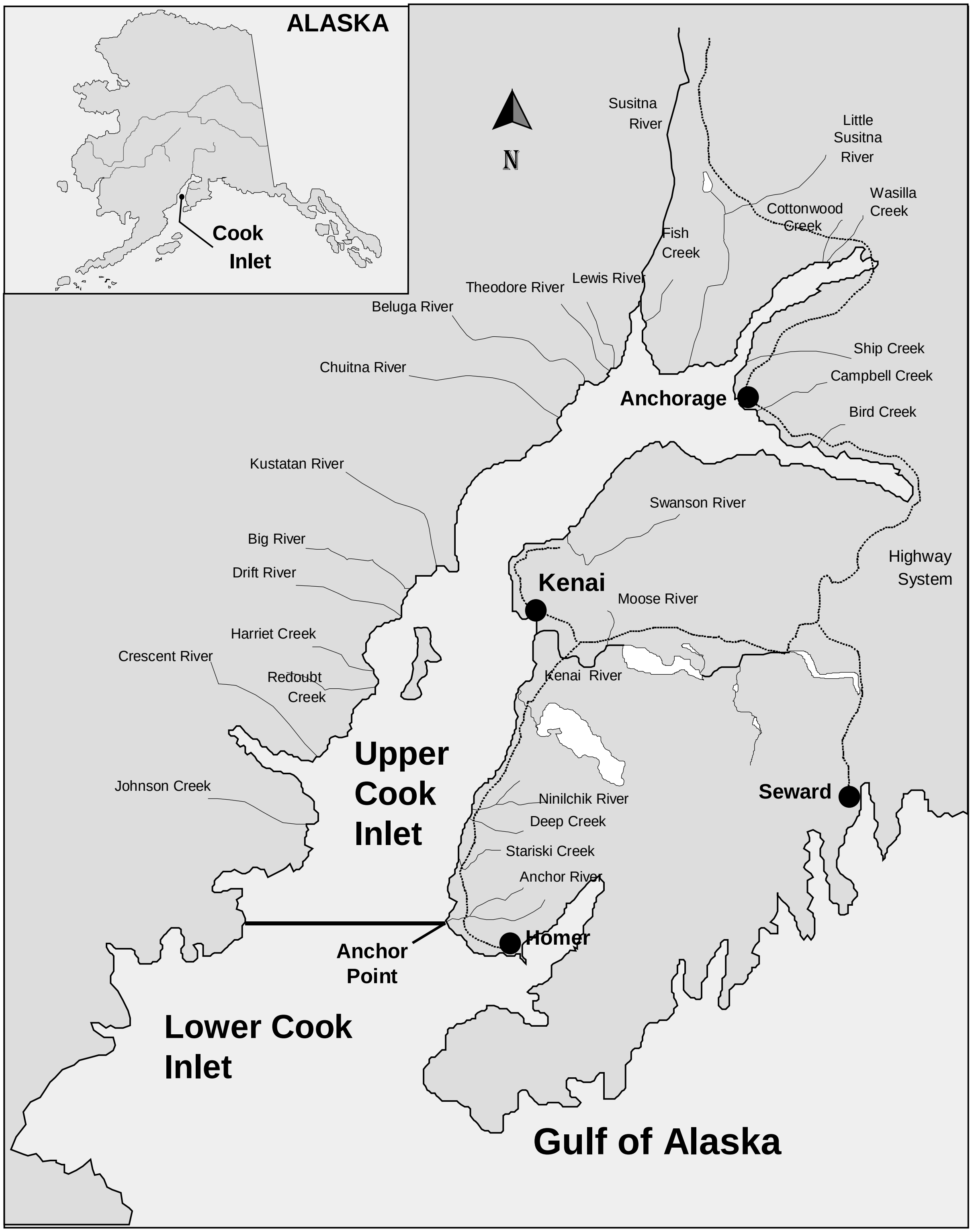
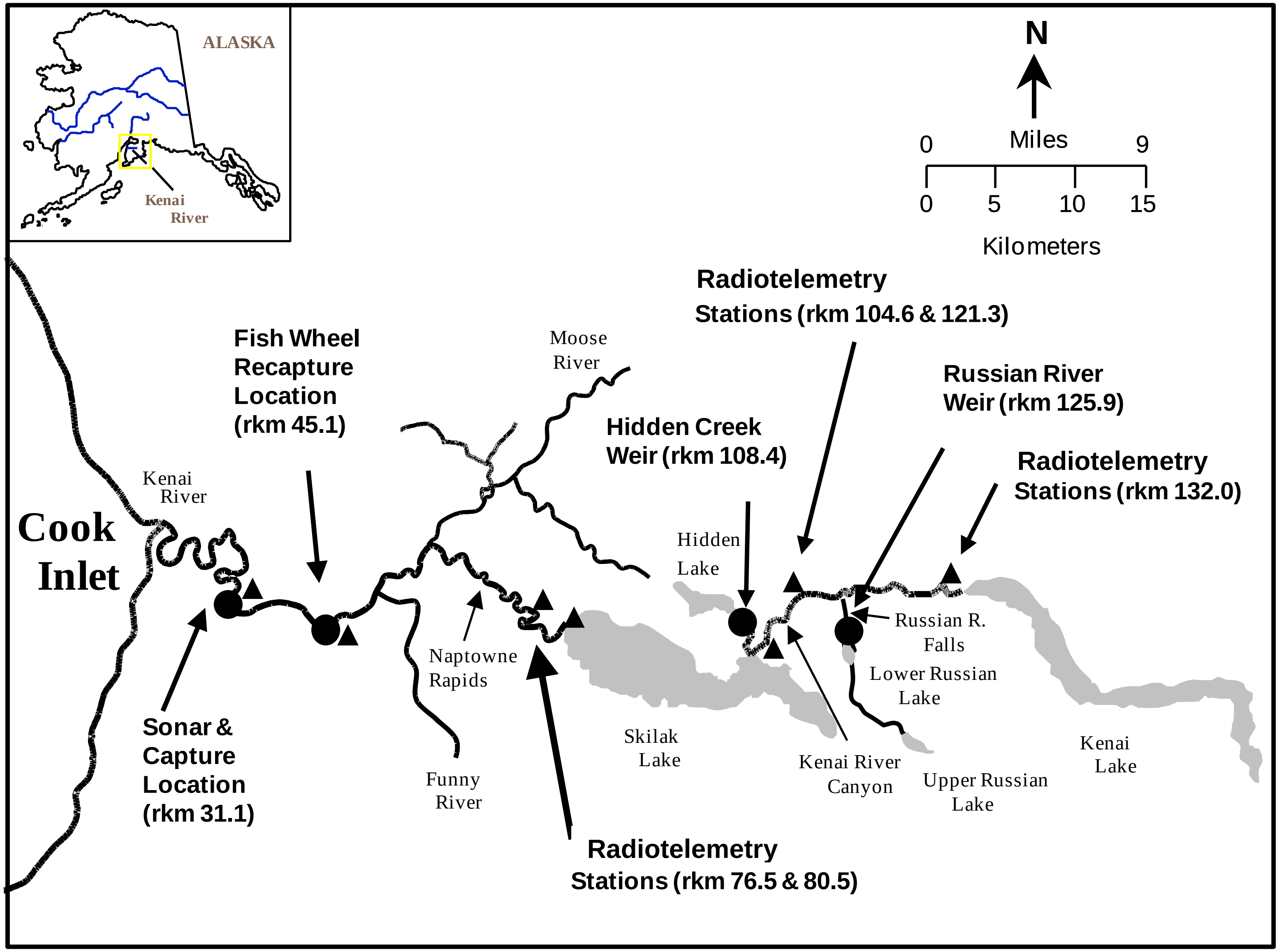
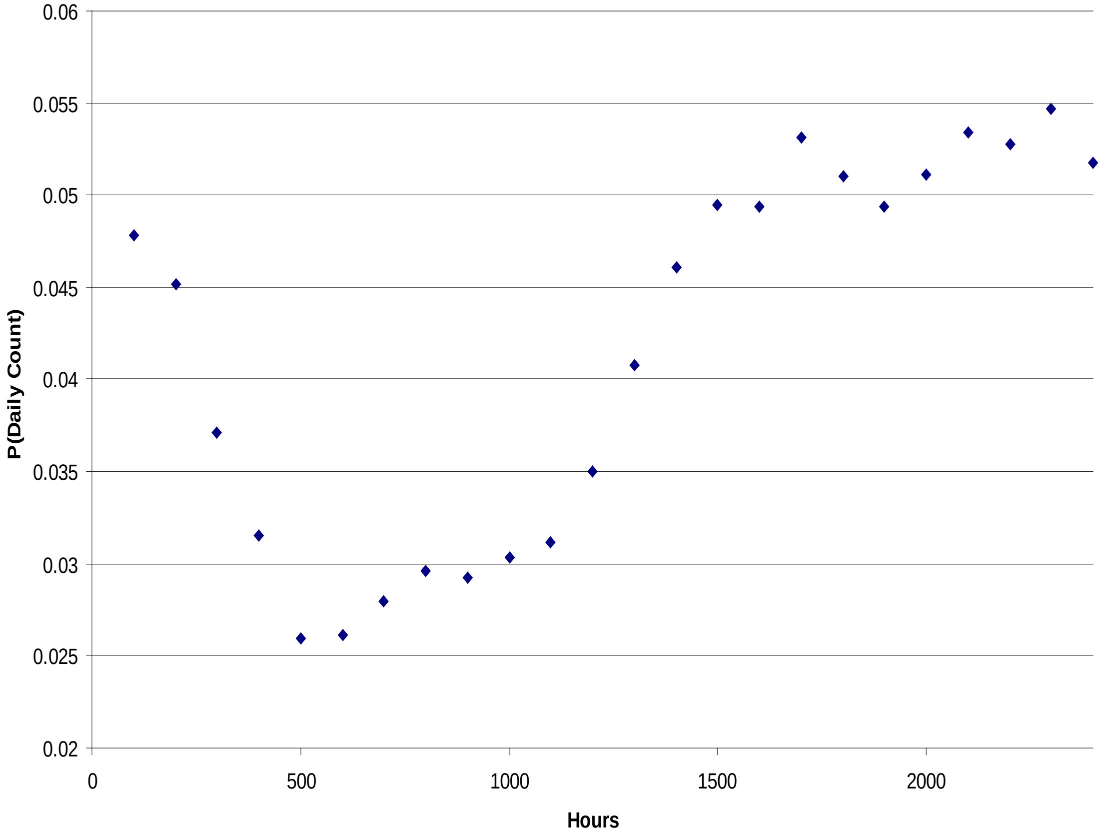


Figure 1.–Map of the Cook Inlet basin indicating location of Kenai River and other selected streams.



Note: Solid circles indicate initial capture and recapture sites for the mark–recapture study. Solid diamonds indicate fixed radiotelemetry sites.

Figure 2.–Map of the study area within the Kenai River watershed.



Note: These data are from 2000.

Figure 3.–Typical plot of proportion of total daily sonar counts observed by hour at rkm 31.1.

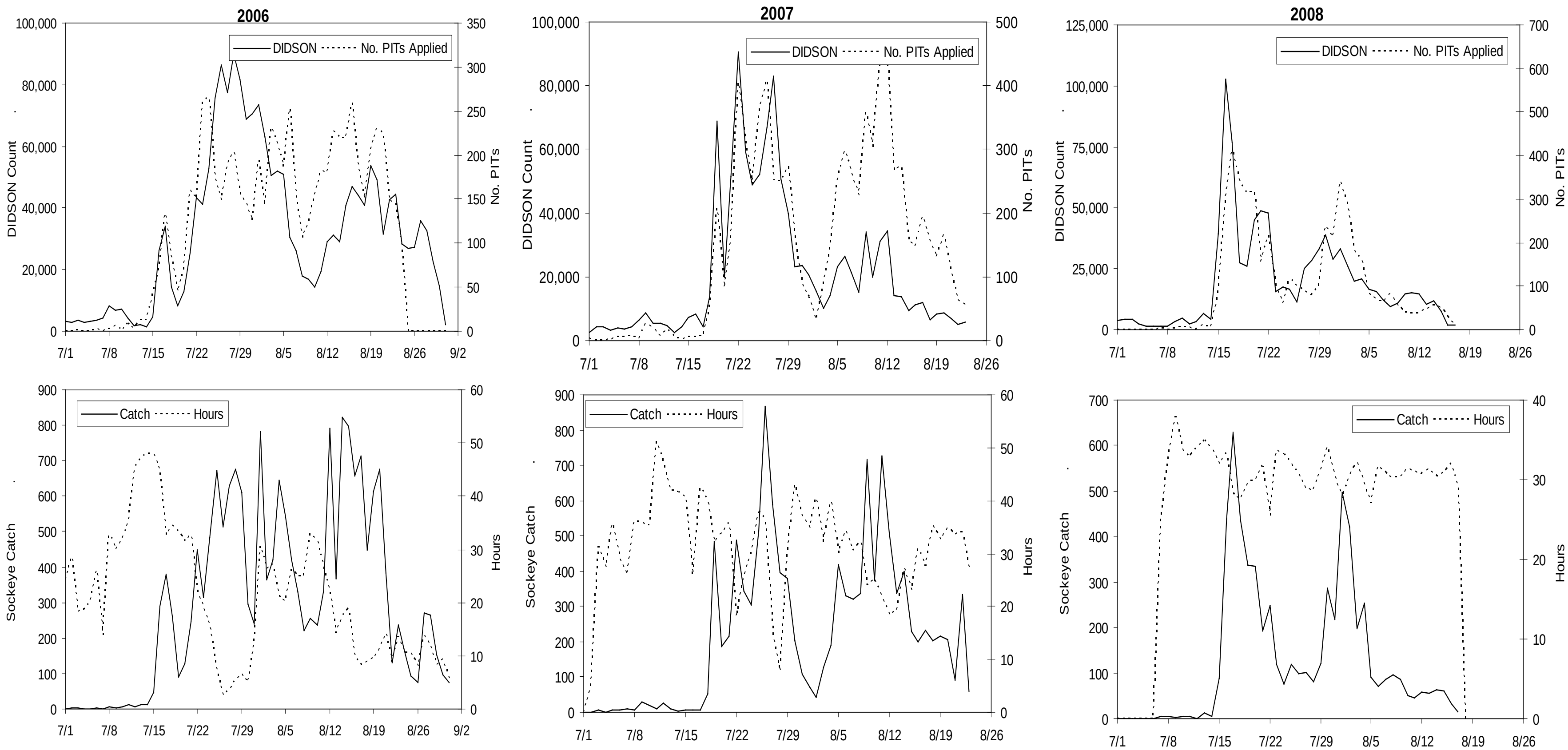


Figure 4.–Daily DIDSON sockeye salmon abundance estimates, number of PIT tags applied, fish wheel catch and fish wheel hours of operation at rkm 31.1, 2006–2008.

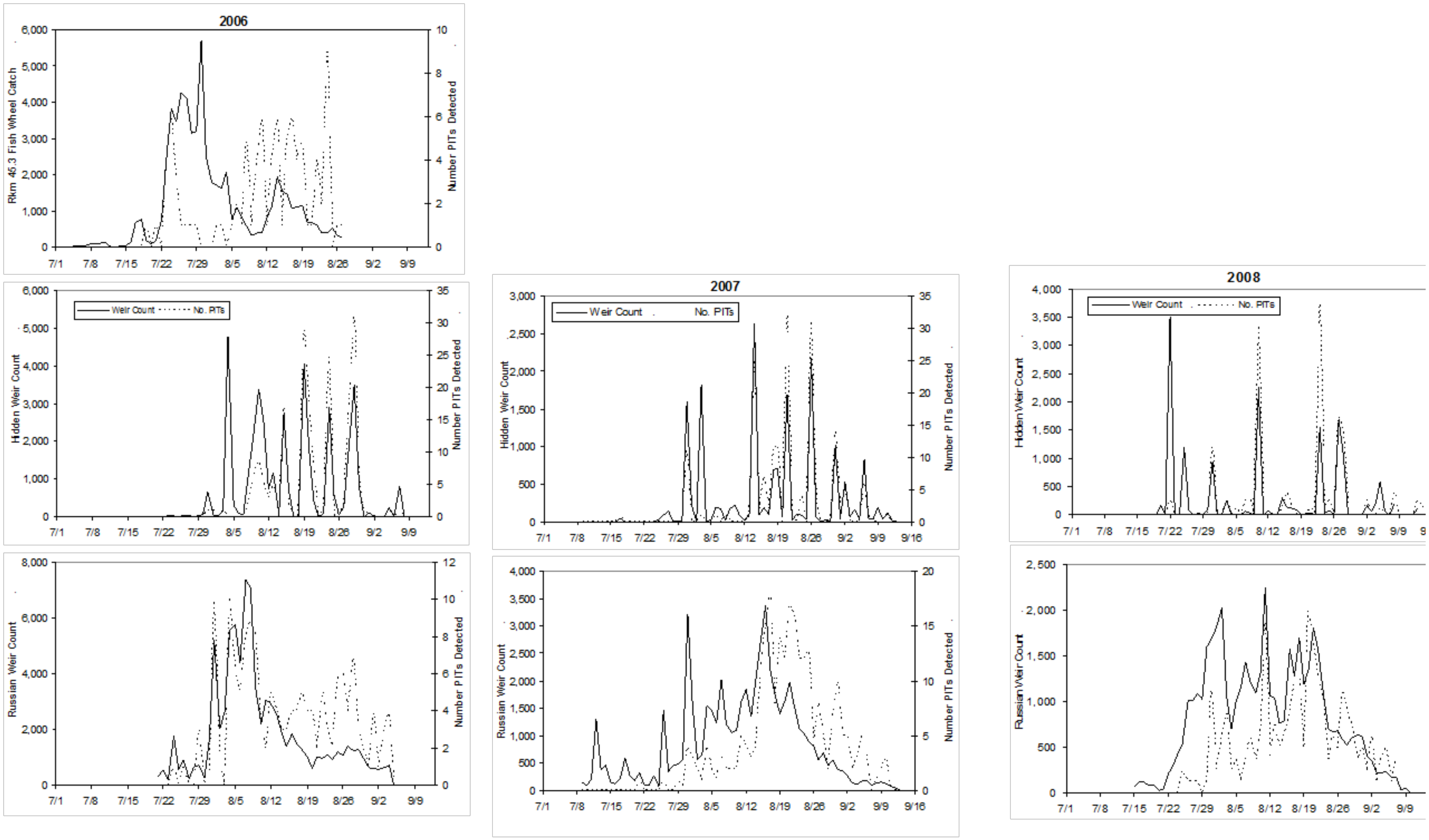


Figure 5.–Daily number of sockeye salmon scanned for tags and number of PIT tags detected at the rkm 45.1 fish wheels and at the Hidden and Russian River weirs, 2006–2008.

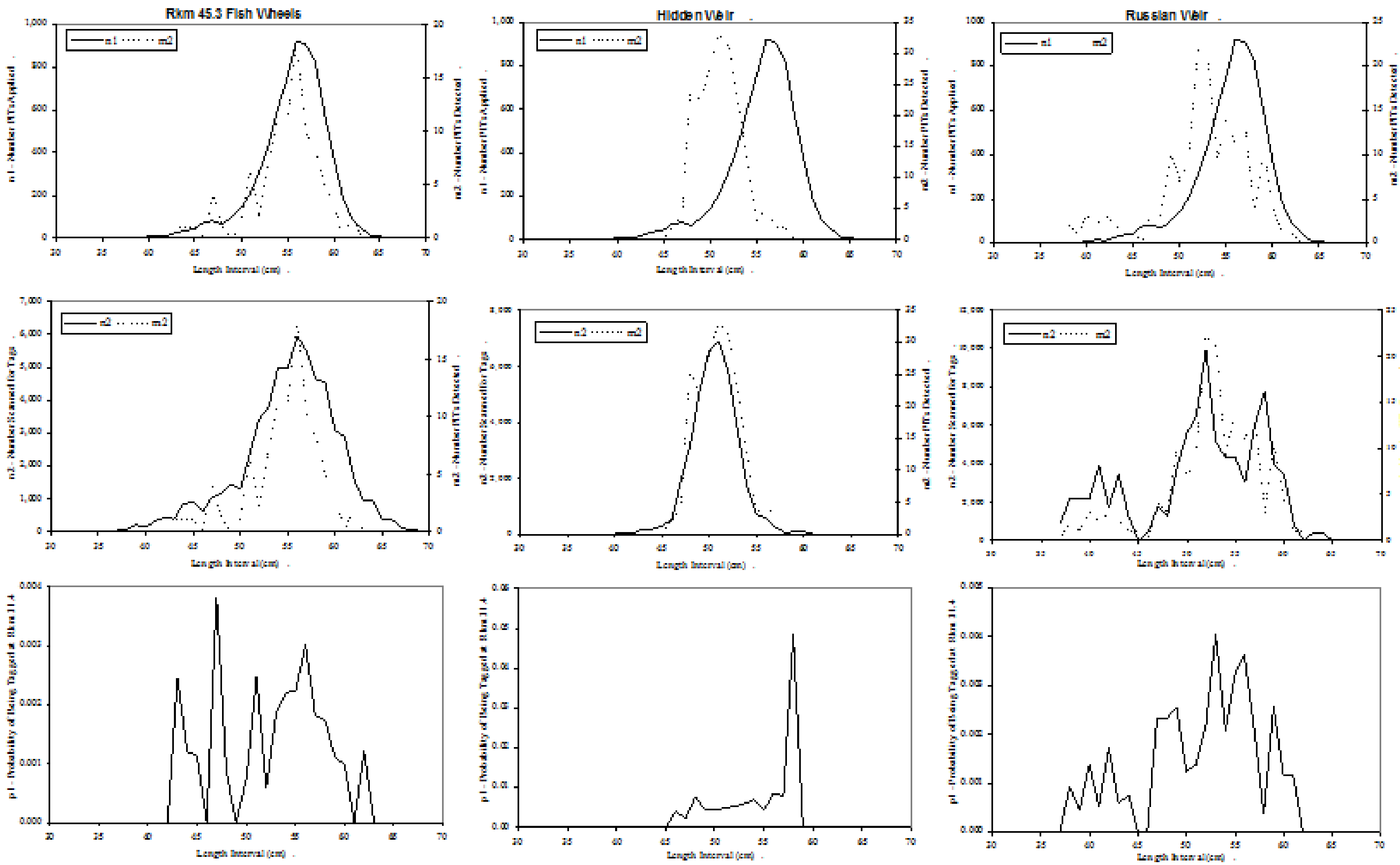


Figure 6.–Number of PIT tags applied at rkm 31.1 (n1), number of sockeye salmon scanned for tags (n2), number of PIT tags detected (m2) at the rkm 45.1 fish wheels, Hidden and Russian river weirs and the probability of being tagged at rkm 31.1 (p1) in relationship to salmon length in 2006.

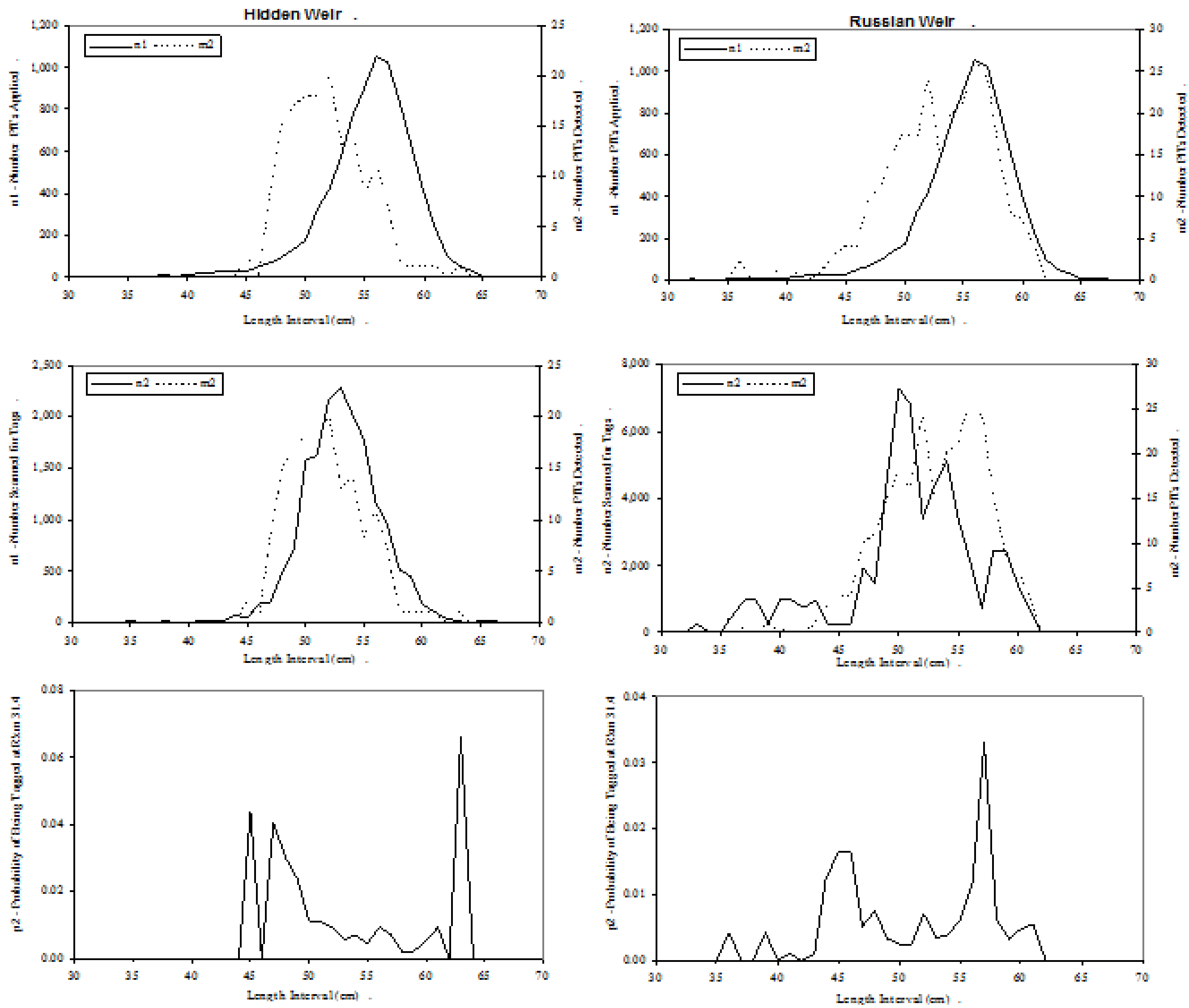


Figure 7.–Number of PIT tags applied at rkm 31.1 (n1), number of sockeye salmon scanned for tags (n2), number of PIT tags detected (m2) at Hidden and Russian river weirs and the probability of being tagged at rkm 31.1 (p1) in relationship to salmon length in 2007.

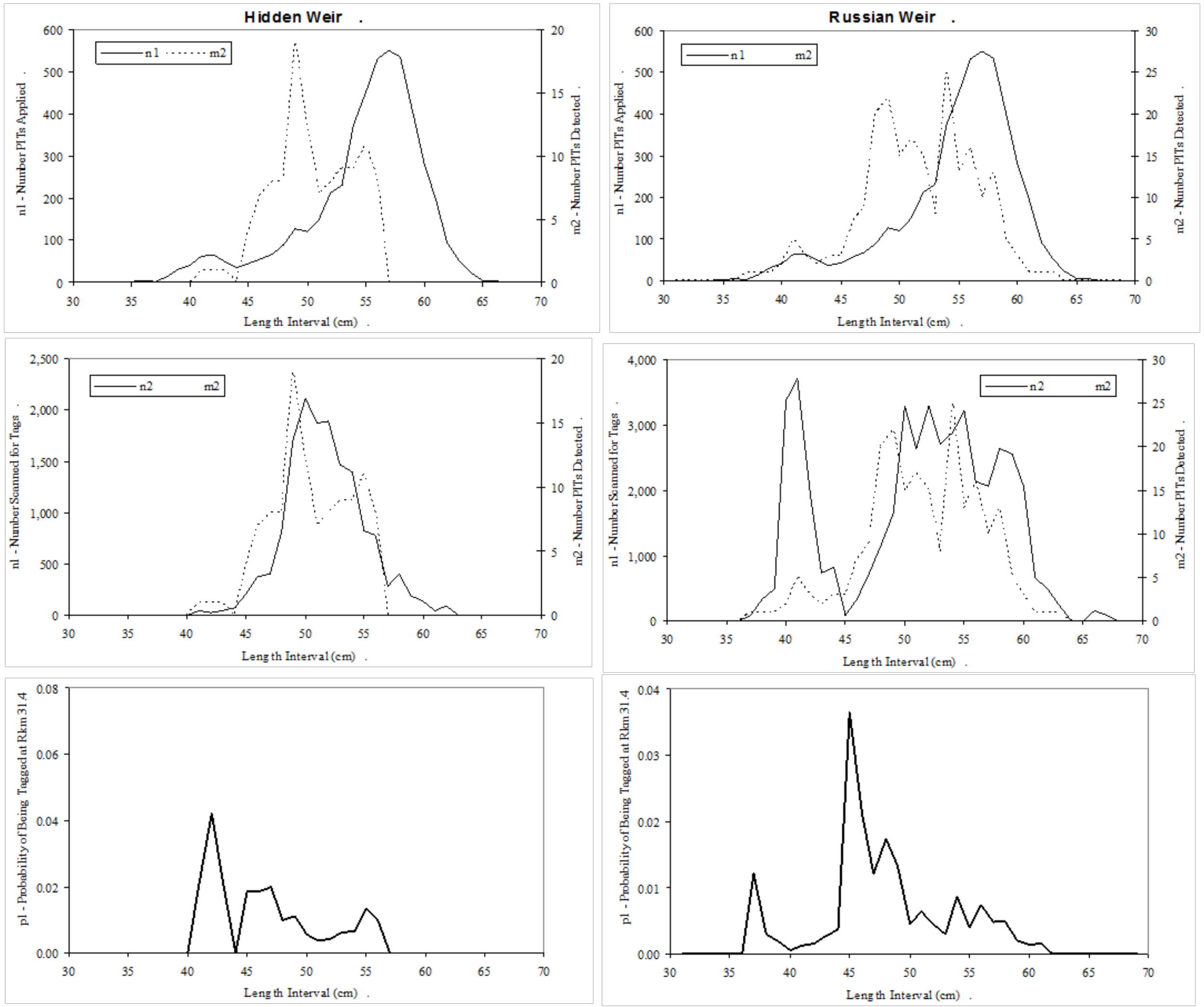
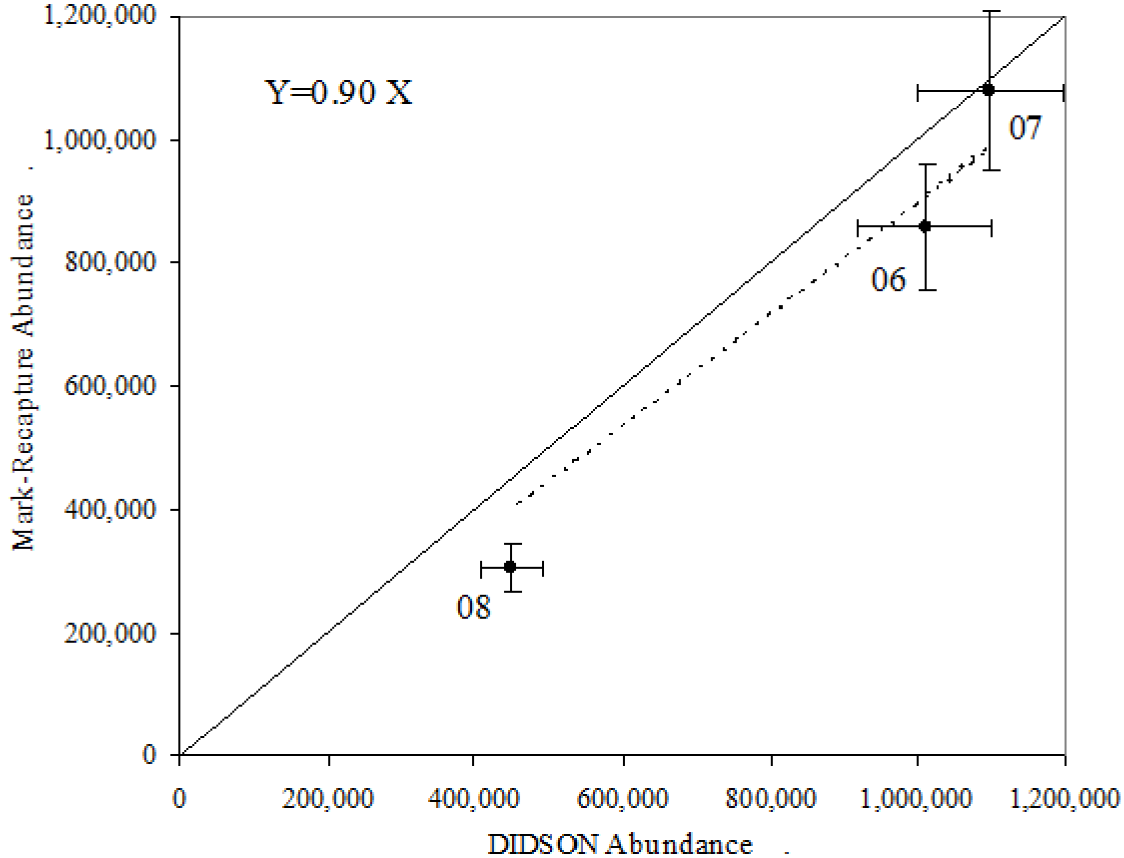


Figure 8.–Number of PIT tags applied at rkm 31.1 (n1), number of sockeye salmon scanned for tags (n2), number of PIT tags detected (m2) at Hidden and Russian river weirs and the probability of being tagged at rkm 31.1 (p1) in relationship to salmon length in 2008.



Note: Abundance estimates included only those fish lengths present at both weirs, i.e. 2006: 470–569 mm, 2007: 450–609 mm, and 2008: 450–569 mm. The error bars in the graph represent 95% confidence intervals. The slope of the regression equation (m=0.90, se=0.07) was not significantly different from one (*P*=0.269).

Figure 9.–Relationship between DIDSON and pooled mark–recapture estimates of sockeye salmon abundance passing rkm 31.1 on the Kenai River, 2006–2008.

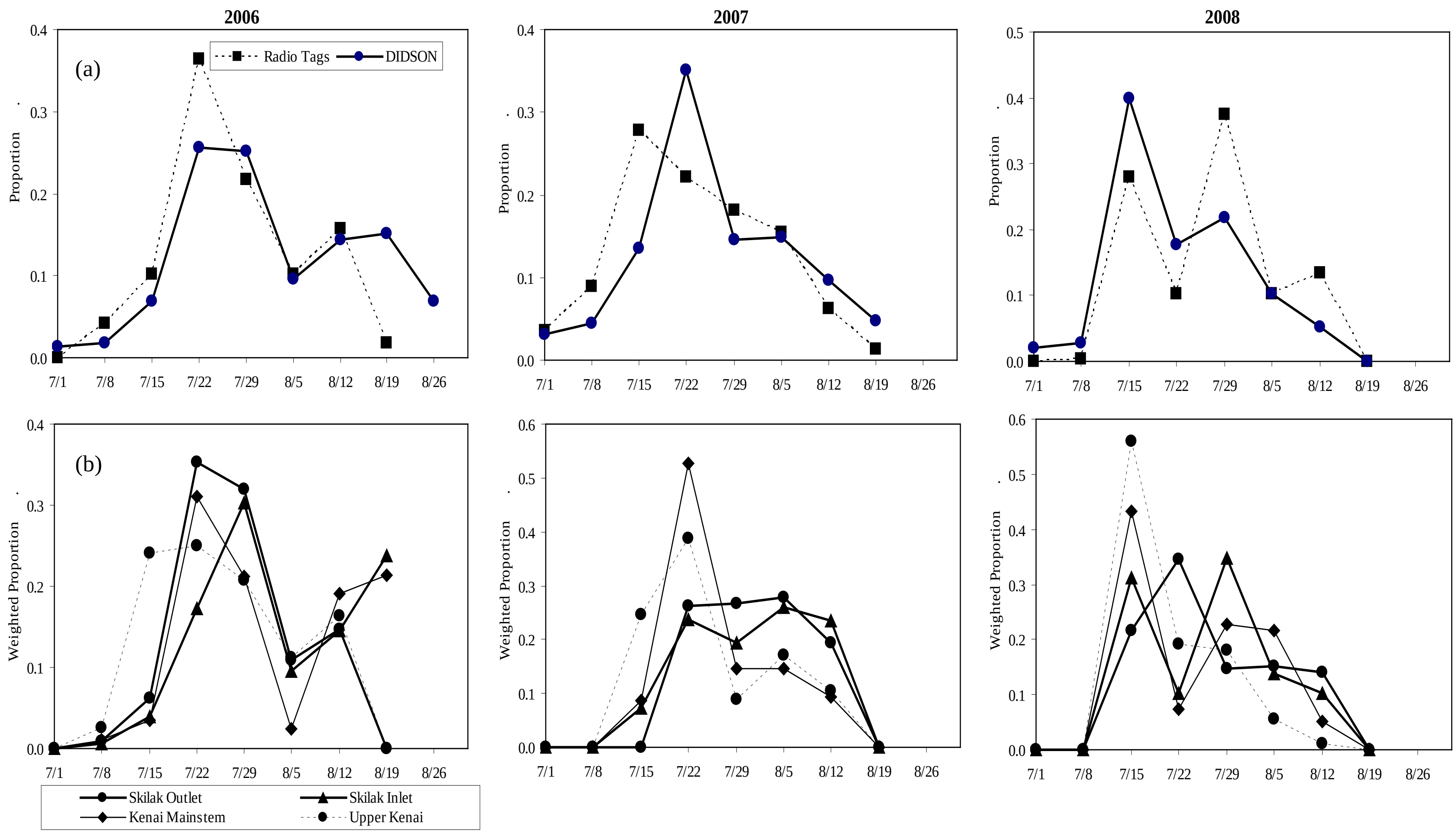
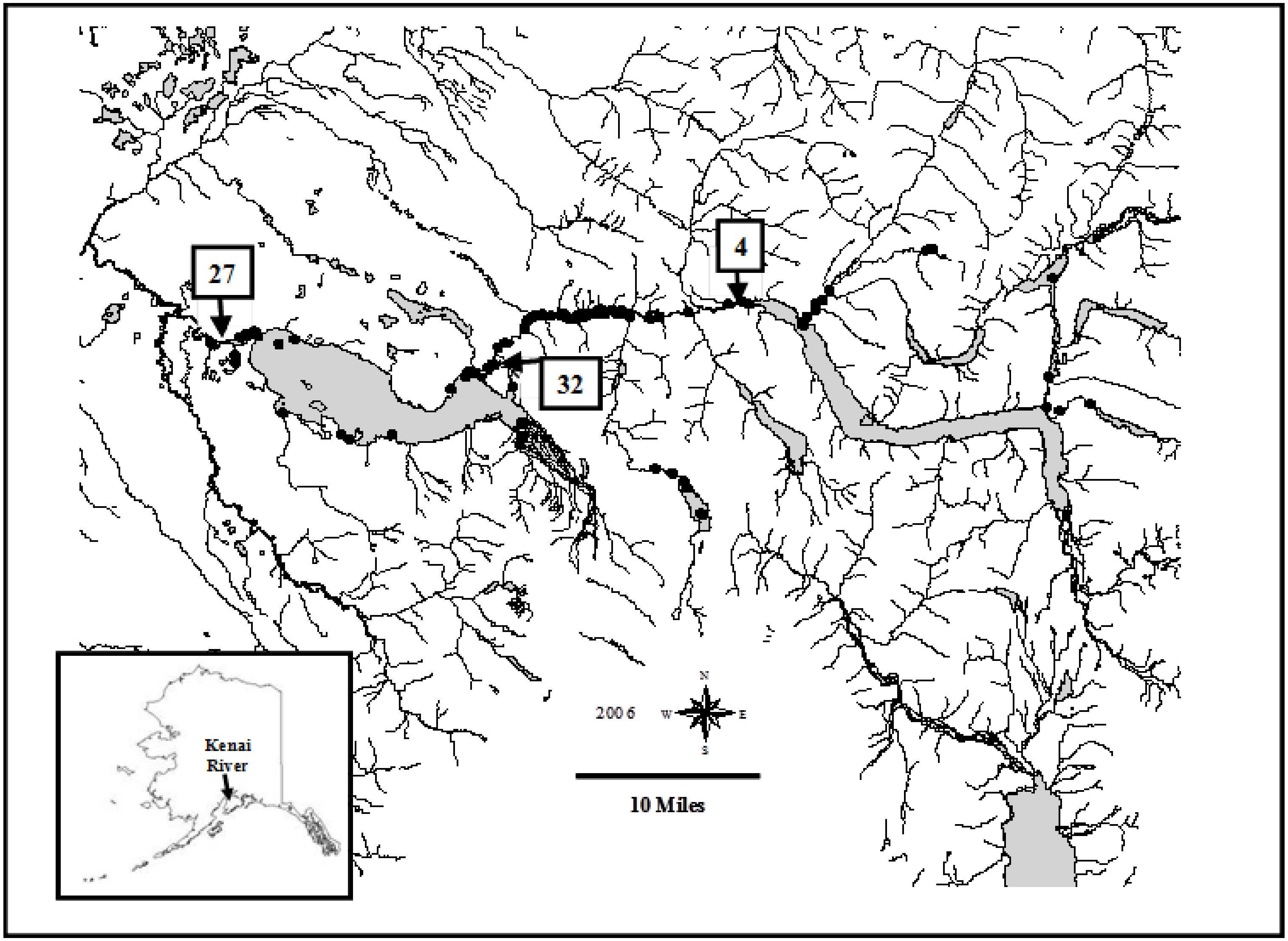
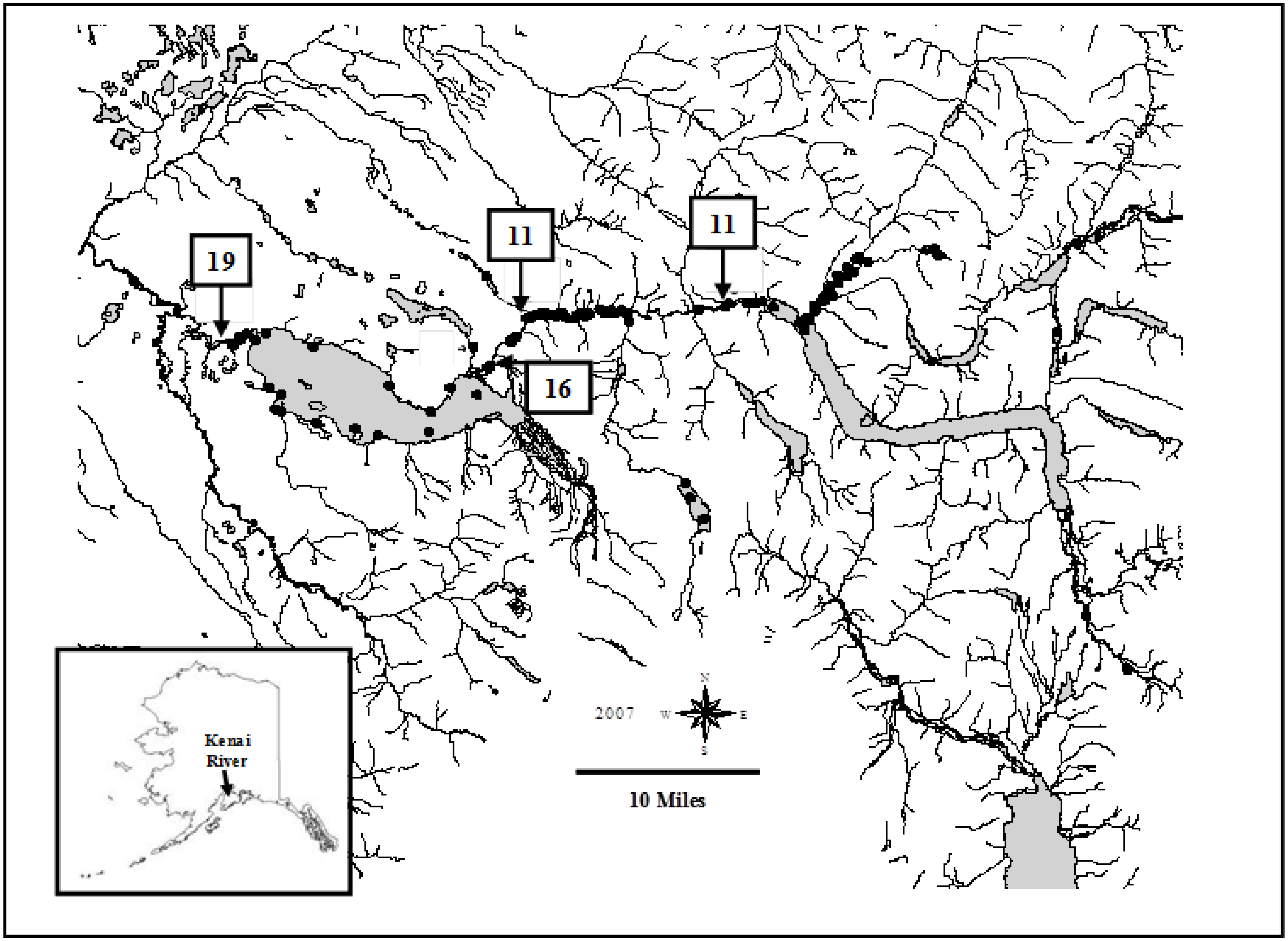


Figure 10.–(a) DIDSON estimates of sockeye salmon passage at rkm 31.1 and number of radio tags applied each week. (b) Weekly weighted proportion of total number of radio tags released at rkm 31.1 and later relocated in 4 major spawning areas within the Kenai River watershed, 2006–2008.



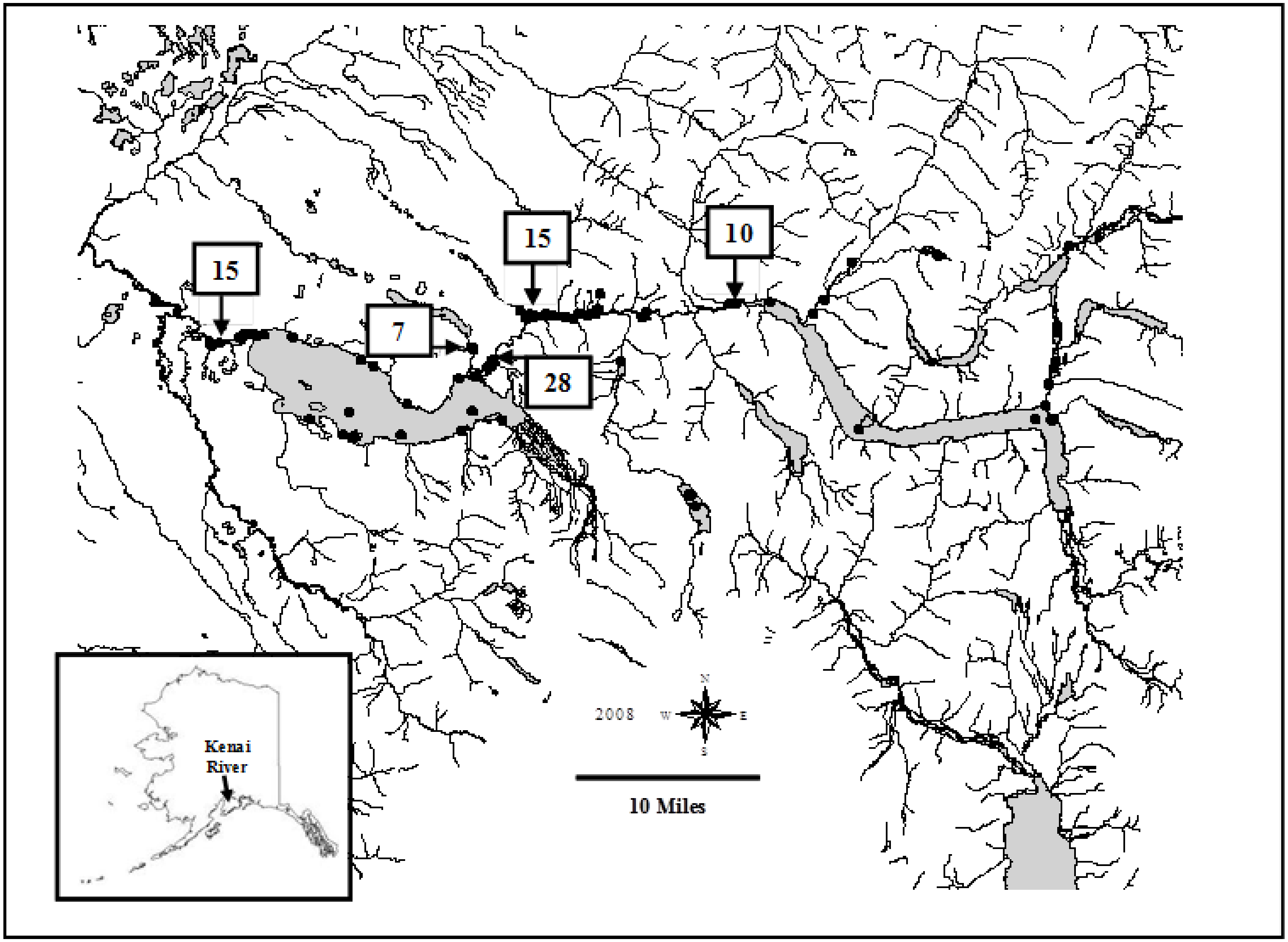
Note: Numbers in boxes indicate multiple tagged fish relocated at the same site.

Figure 11.–Final destinations of radiotagged sockeye salmon (solid circles) in the Kenai River watershed in 2006.



Note: Numbers in boxes indicate multiple tagged fish relocated at the same site.

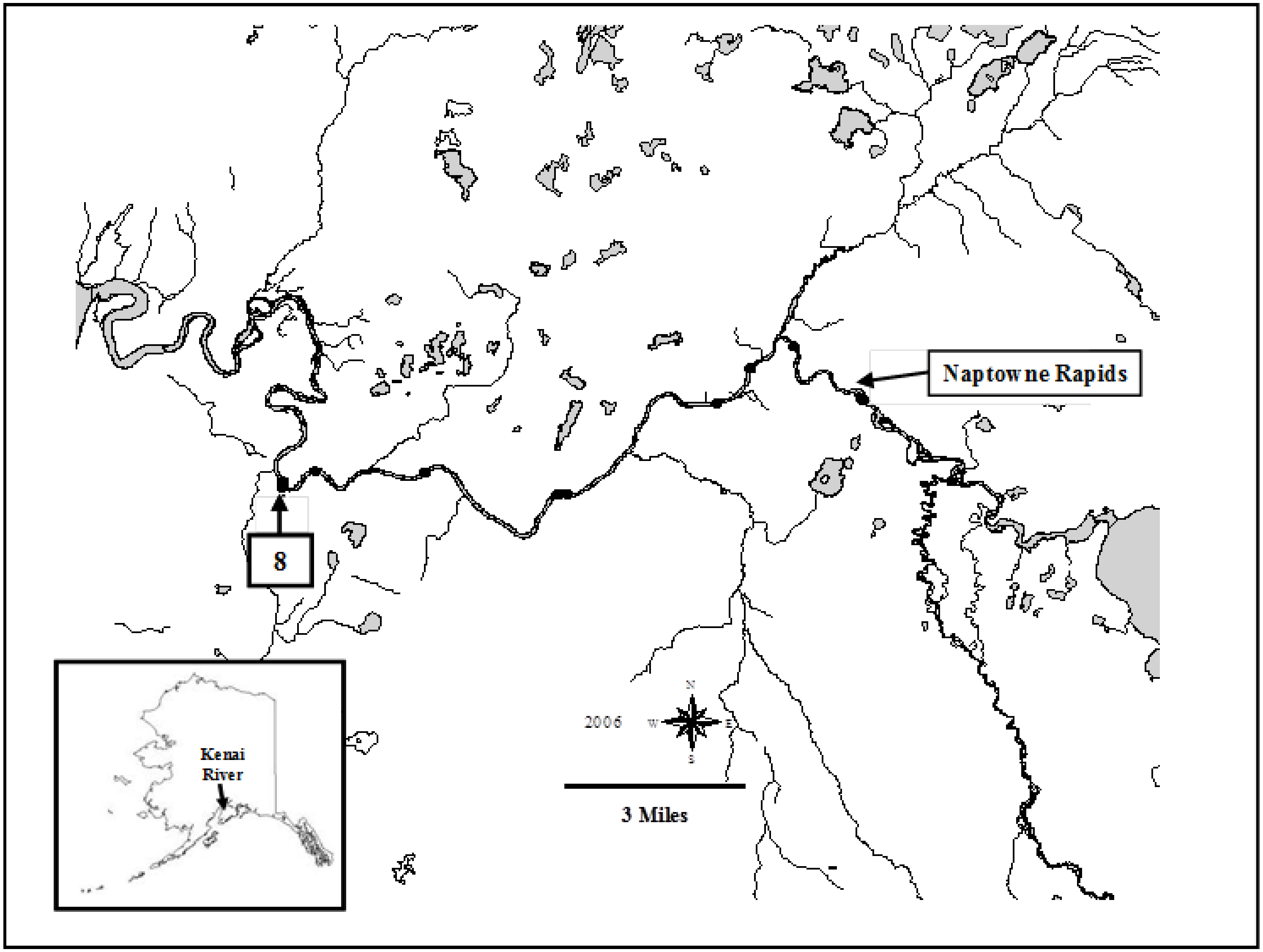
Figure 12.–Final destinations of radiotagged sockeye salmon (solid circles) in the Kenai River watershed in 2007.



Note: Numbers in boxes indicate multiple tagged fish relocated at the same site.

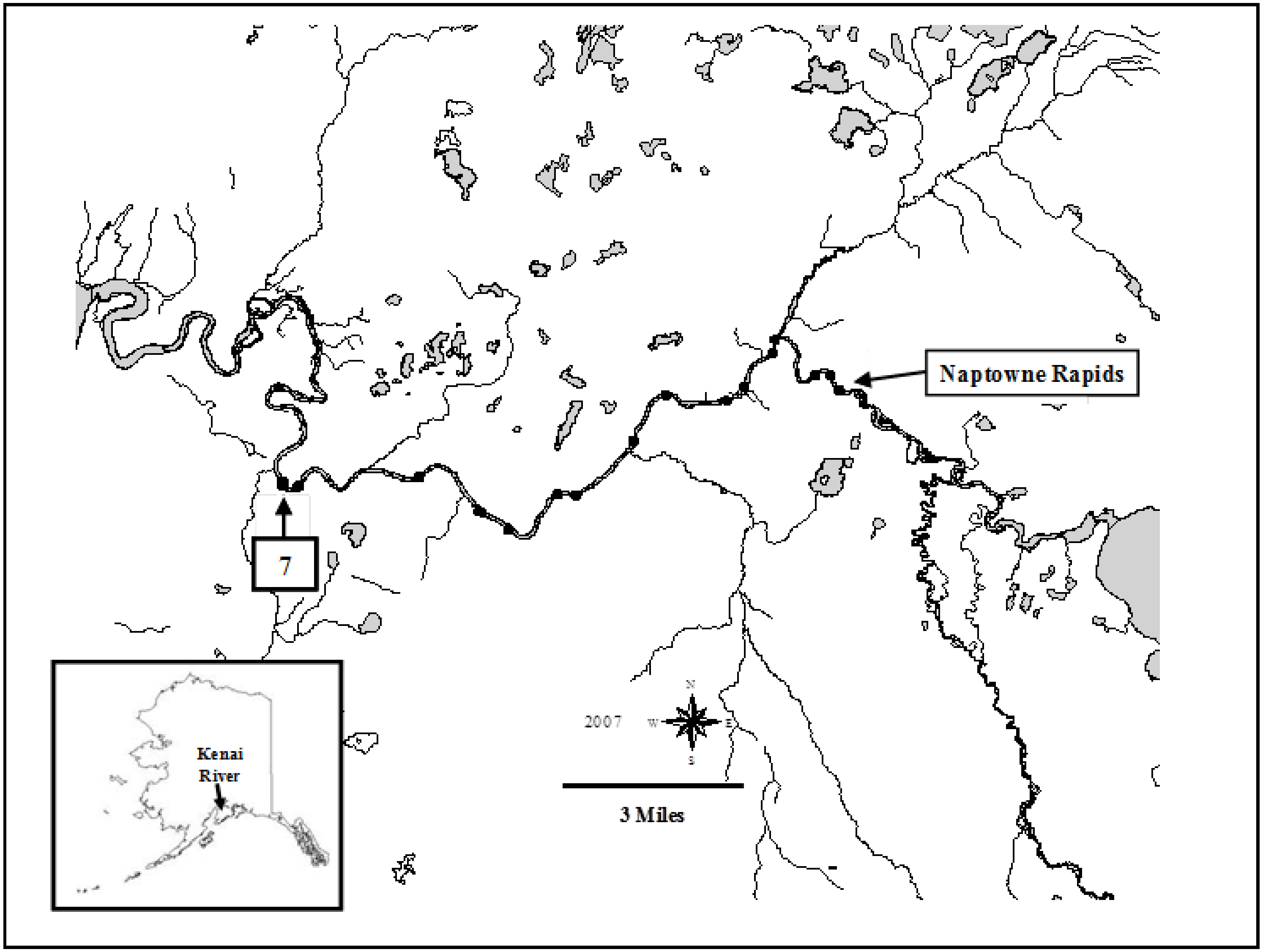
Figure 13.–Final destinations of radiotagged sockeye salmon (solid circles) in the Kenai River watershed in 2008.

APPENDIX A



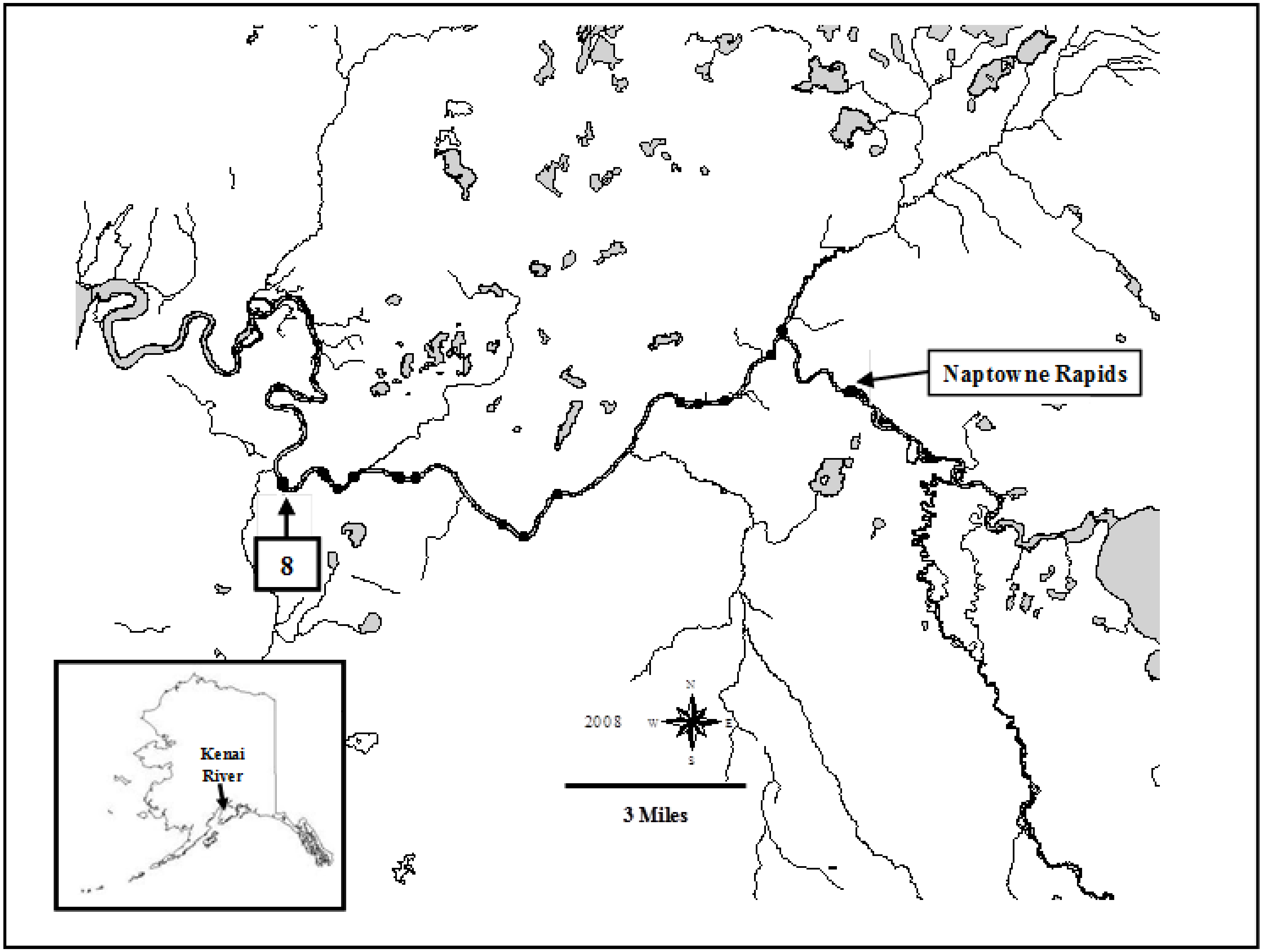
Note: Numbers in boxes indicate multiple tagged fish relocated at the same site.

Appendix A1.–Final destinations of radiotagged sockeye salmon (solid circles) in the Kenai River watershed that apparently died before reaching their spawning grounds in 2006.



Note: Numbers in boxes indicate multiple tagged fish relocated at the same site.

Appendix A2.–Final destinations of radiotagged sockeye salmon (solid circles) in the Kenai River watershed that apparently died before reaching their spawning grounds in 2007.



Note: Numbers in boxes indicate multiple tagged fish relocated at the same site.

Appendix A3.–Final destinations of radiotagged sockeye salmon (solid circles) in the Kenai River watershed that apparently died before reaching their spawning grounds in 2008.