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A Radiotelemetry Investigation of the Spawning Origins of Innoko River Inconnu (Sheefish)

by

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And

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September 2012

Alaska Department of Fish and Game

Divisions of Sport Fish and Commercial Fisheries

Symbols and Abbreviations

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Weights and measures (metric)

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

Weights and measures (English)

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

Time and temperature

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

Physics and chemistry

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

General

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

Mathematics, statistics

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

FISHERY DATA SERIES NO. 12-54

A RADIOTELEMETRY INVESTIGATION OF THE SPAWNING ORIGINS OF INNOKO RIVER INCONNU (SHEEFISH)

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ABSTRACT

Radiotelemetry techniques were used to identify the spawning origins of inconnu captured in the Innoko River drainage during the summer feeding season during this six year study. Tracking flights were conducted prior to and during the spawning season in the Innoko River and in the five Yukon drainage spawning areas identified by previous studies. Several remote radio receiving stations were used to monitor movement into and out of the Innoko drainage and the known spawning areas. Data from remote radio receiving stations revealed that inconnu left the Upper Innoko River drainage between mid-July and late-August. Tagged inconnu entered the Koyukuk River during July and August and were again detected at the Koyukuk station in late October as they migrated downstream. Inconnu passed the Middle Yukon station in September on their way upstream to spawn and again in mid-October on their way back downstream. During September, aerial surveys located most (58%) radio-tagged fish near the Yukon mainstem spawning area in the Yukon Flats, 19% near the Koyukuk (Alatna) River spawning area and a few fish (3%) within the Nowitna (Sulukna) River spawning area. No radio-tagged inconnu from the Innoko River were found during the spawning season in the Tanana River spawning sites. Seventeen percent of inconnu tagged in the Innoko River drainage during the summer feeding season were located at a new spawning site identified in the Upper Innoko River drainage near Folger Creek. Length, genetic, and maturity samples were collected from inconnu from this new site. Nearly all inconnu in this study exhibited very strong spawning site fidelity. However, we documented two instances of individual fish spawning in consecutive years in different sites. The empirical annual survival rate for radio-tagged fish averaged 0.65.

Key words: Sheefish, Inconnu, *Stenodus leucichthys,* radio telemetry, Yukon River, Innoko River, Koyukuk River, Alatna River, Nowitna River, Sulukna River, spawning areas, spawning frequency, migration speed, spawning fidelity seasonal movements.

INTRODUCTION

The Innoko River is a large, slow flowing, meandering river draining into the Lower Yukon River. Inconnu are common in the river and are a dependable food resource for residents of the area (Brown et al. 2005). Alt (1983) studied inconnu in the Innoko River for two years and hypothesized that they used the drainage for feeding but migrated farther up the Yukon River to spawn. If this hypothesis were true, then all inconnu found in the Innoko River would be members of distant upstream spawning populations. In this multi-year study we used radiotelemetry techniques to test our primary hypothesis that all inconnu feeding in the Innoko River drainage during spring and summer were members of known populations with spawning origins in upstream locations in the Yukon River drainage. Because upstream spawning populations are known to be anadromous (Brown et al. 2007; Esse 2011), some fraction of each population would be expected to migrate into the Innoko River to feed during summer. It was therefore possible that the proportions of upstream spawning populations in our radio-tagged sample reflected the relative abundances of the contributing populations. In addition, we report on migration timing, migration rates, annual survival, and spawning frequency of radio-tagged inconnu.

Prior to this study, five inconnu *Stenodus leucichthys* spawning areas had been identified in the Alaska portion of the Yukon River drainage: two in the Upper Koyukuk River (Alt 1969); one in the Chatanika River, a tributary of the Tanana River; one in the mainstem Yukon River upstream from the Porcupine River mouth (Brown 2000), and one in the Sulukna River, a tributary of the Nowitna River (Alt 1985; Gerken 2009; Figure 1). Alt (1987) suspected two or three additional inconnu spawning areas in the upper reaches of the Yukon River drainage as well, upstream from the Yukon Flats region, but these have not been confirmed. Analysis of strontium (Sr) concentration levels in fish otoliths is an effective method of identifying anadromous fish captured in freshwater (Campana 1999; Howland et al. 2001; Brown and Severin 2009). Brown et al. (2007) and Esse (2011) conducted otolith Sr analyses on inconnu harvested from spawning migrations into the Upper Koyukuk, Yukon Flats, Tanana River, and Nowitna River and found that at least some anadromous individuals were present in the spawning populations within all of these drainages. Our failure to locate additional inconnu spawning populations, despite widespread sampling throughout the drainage since the 1960s, suggested that the five identified inconnu spawning areas represented all spawning habitat in the drainage downstream from the Upper Yukon Flats, approximately 1,700 km from the sea. Further, if all inconnu in the drainage originated in one of the five known spawning areas, as hypothesized, and the ranges of these populations extended from upstream spawning grounds to the ocean, then virtually all of the fisheries in the drainage were targeting one or more of these same five populations.

At the present time, it is not possible to effectively monitor or manage inconnu populations in the Yukon River drainage. While it may be true that inconnu throughout the drainage come from one of the five known spawning areas, we don't fully understand annual migration patterns along the river or the distribution of the various demographic groups within the drainage. We don’t know the relative abundances of the different spawning populations, nor do we know spawning frequency once a fish becomes mature, or the annual spawning proportion of mature individuals for any population. As such, interpretation of estimates of spawning abundance would be difficult even if they could be achieved. Inconnu populations appear to be sustaining themselves, based simply on the fact that people continue to catch them throughout their known range, but there is no formal monitoring mechanism in place.

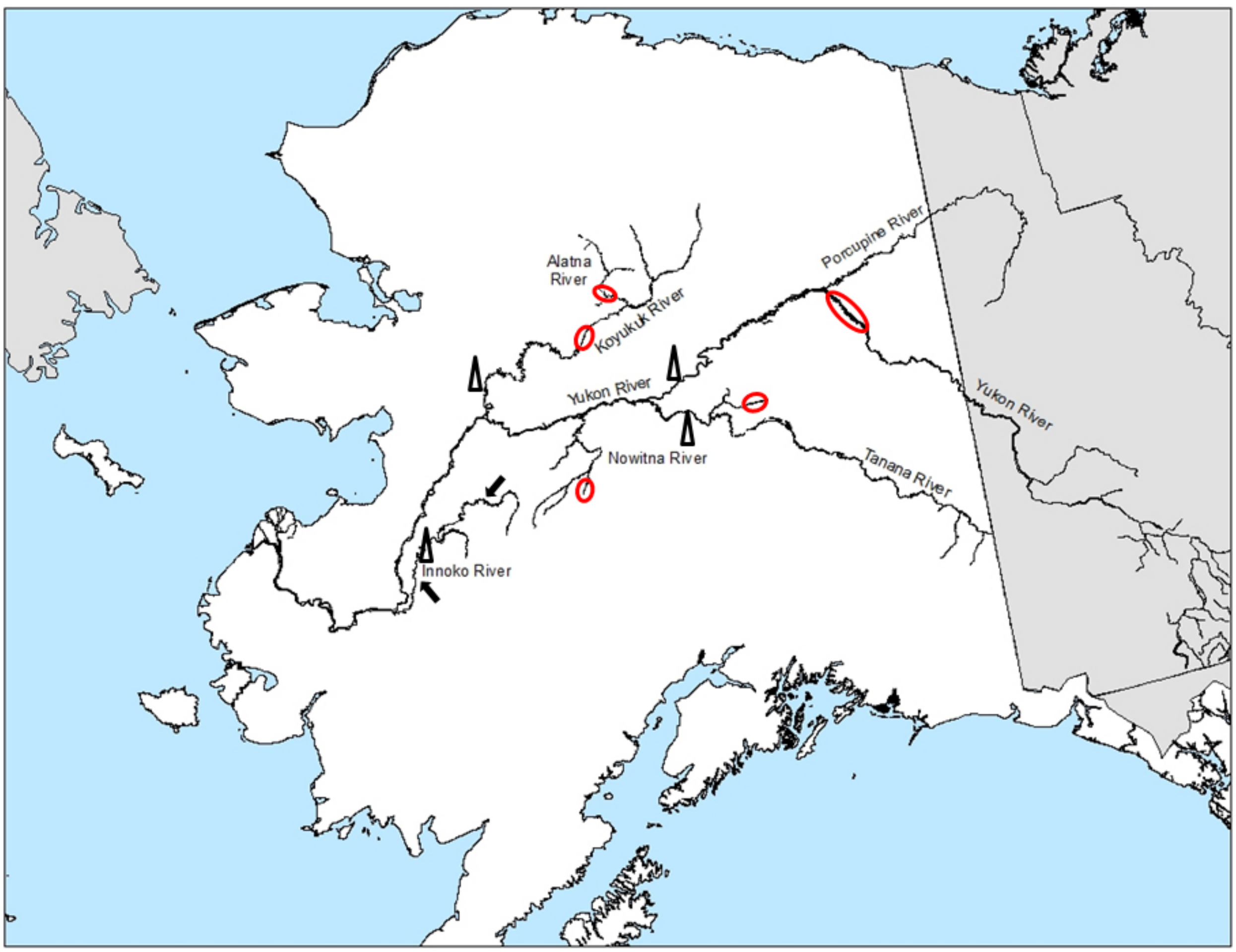

Figure 1.–The Yukon River drainage in Alaska and Yukon Territory with major tributaries labeled: 1) locations of previously identified inconnu spawning areas indicated with elipses; 2) tagging sites in the Innoko River drainage indicated with arrows; and, 3) locations of the four remote radio receiving stations indicated with tall triangles.

It is possible to deplete inconnu populations, as demonstrated in the Great Slave Lake in Canada where inconnu populations have been severely impacted by commercial fisheries during the last 60 years. Both Dymond (1943) and Fuller (1955) reported that tremendous spawning migrations of inconnu took place in at least five rivers flowing into the south side of Great Slave Lake, including the Hay, Buffalo, Little Buffalo, Slave, and Talston rivers. Traditional subsistence fisheries within these rivers harvested great numbers of inconnu each fall, apparently without depleting them. Commercial fishing in Great Slave Lake began in 1945 (Kennedy 1956; Keleher 1972; Roberge et al. 1982). Historically, inconnu did not exceed 10% of the total commercial harvest, the primary species of interest being lake whitefish *Coregonus clupeaformis* and lake trout *Salvelinus namaycush*. While there has been a stable market for inconnu as a smoked product, their populations are thought to have been seriously depleted by both the commercial fishery and in-river subsistence fisheries (Cosens et al. 1993; Van Gerwen-Toyne et al. 2010). Inconnu spawning populations currently exist in the Slave River, where the population appears to be stable (Tallman et al. 2005), and the Buffalo River, where the population appears to be at risk of extinction (Van Gerwen-Toyne et al. 2010). Inconnu populations are thought to have been extirpated from the Hay, Little Buffalo, and Talston rivers, primarily due to overfishing in the commercial fishery. Efforts are underway to minimize inconnu bycatch in the commercial fishery in an attempt to save the two remaining populations. Similar to the Great Slave Lake fishery, inconnu are taken as bycatch in the Yukon River salmon fisheries and are harvested in sport and traditional fisheries throughout the drainage. Also similar to the Great Slave Lake fishery, where commercial lake trout and lake whitefish fisheries continue despite the depleted inconnu populations, it is unlikely that the salmon fisheries in the Yukon River would be curtailed by a decline in inconnu populations.

STUDY AREA

The Innoko River is a large tributary of the Lower Yukon River, entering the Yukon River approximately 473 km upstream from the Bering Sea (Figure 2). It drains an area of about 28,230 km^2, which is approximately 3.3% of the entire Yukon River drainage basin (Alt 1983; Brabets et al. 2000). The Innoko River is connected to the Yukon River at its primary mouth in Red Wing Slough near the village of Holy Cross and its secondary mouth, Paimiut Slough, 44 km downstream along the Yukon River. In addition, Yukon River water joins the Innoko River approximately 118 and 163 km upstream from the mouth through Shageluk and Holikachuk sloughs respectively. Upstream of this connection with the Yukon River, the Innoko to the North Fork Innoko River is stained from wetland seepage but is generally not silty. Near the mouth of the North Fork Innoko River, the drainage transitions from a slow, stained, meandering river flowing over a mud or sand substrate to one that flows swift and clear over a gravel substrate for most of its remaining length (Alt 1983). The topography changes from flatland with an occasional hill near the river to one in which the river is bounded between hills and mountains on both banks. The Innoko River drainage supports a wide range of fish habitats including slow moving deep channels, more than 26,000 lakes (many of which maintain stream connections with the river), and clear swift moving, pool-riffle streams.

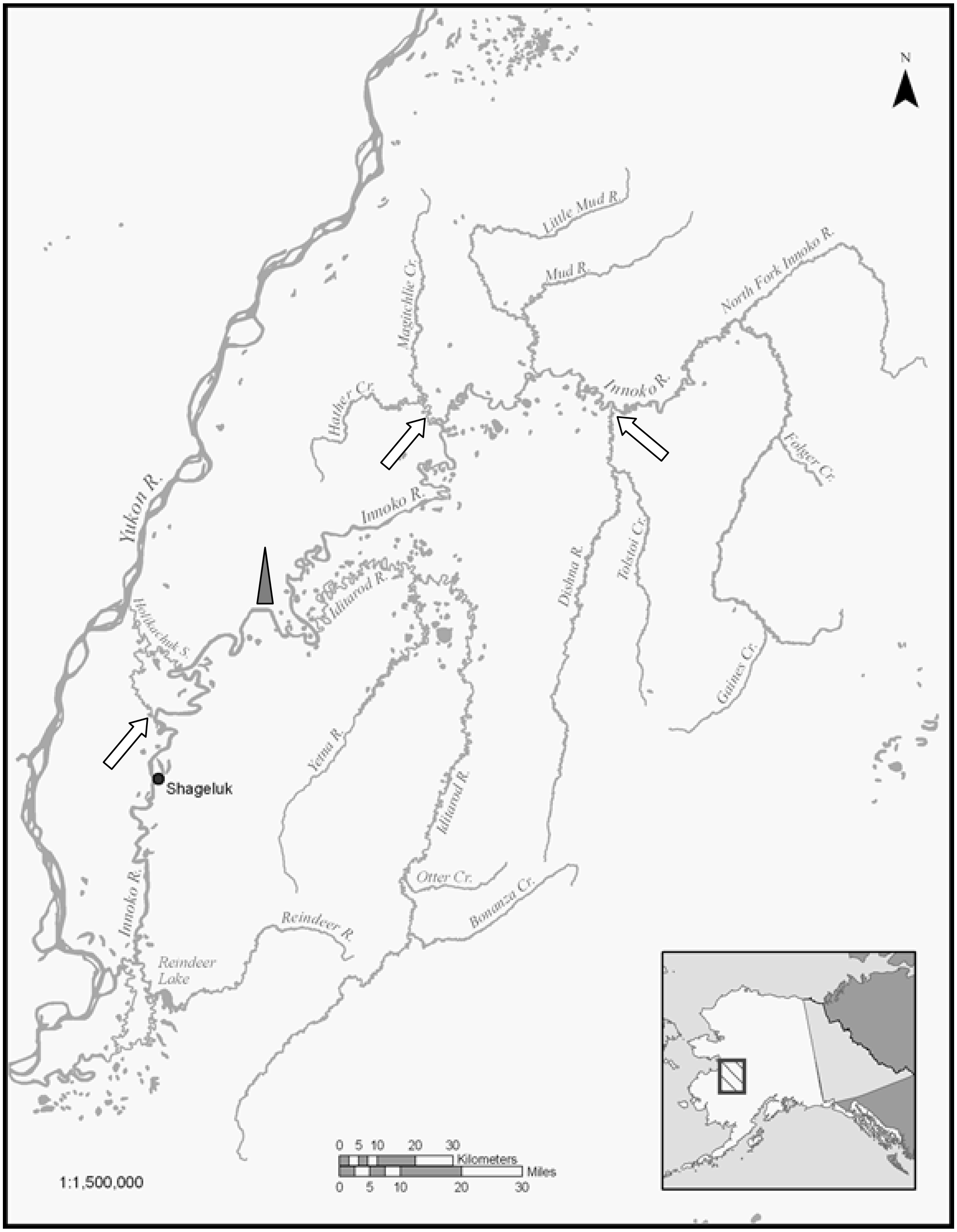

Figure 2.–The Innoko River in the Lower Yukon River drainage identifying major tributaries and the location of Shageluk, the one community in the drainage. Inconnu were tagged at several locations between the mouths of Hather Creek and the Dishna River in the upper drainage (see arrows), and near the confluence of the Innoko River and Holikachuk Slough in the lower drainage (see arrow). A remote radio receiving station was located downstream from the mouth of the Iditarod River in the lower drainage (triangle).

OBJECTIVES

1. Identify the spawning origins of inconnu radio-tagged in the Innoko River during summer by surveying known and suspected spawning areas in the drainage during spawning season;
2. Determine spawning frequency of radio-tagged inconnu by locating fish on spawning grounds over the course of four or more spawning seasons;
3. Estimate annual survival of radio-tagged inconnu empirically by assessing the status of each tagged fish over time; and,
4. Estimate the proportional contributions of identified spawning populations to the aggregation of feeding inconnu in the Innoko River during 2007 through 2009.

METHODS

Candidate inconnu for radio tagging were selected based on minimum size criteria for inconnu maturity of the Yukon River mainstem population. Brown (2000) reported that mature male inconnu from the Yukon River population ranged between 61 and 85 cm fork length (FL) while mature females ranged between 71 and 103 cm FL. Inconnu 65 cm FL or greater were therefore likely to be mature and were considered to be good candidates for radio tagging. Unknown proportions of male and female inconnu were selected because during the summer feeding season when they were tagged it was not possible to distinguish sex from external characteristics. Transmitters were expected to be deployed in both spawners and mature nonspawners. Fish captured in early summer that are preparing to spawn during the upcoming fall are indistinguishable from those that are not. Inconnu are thought to spawn every two or three years once they become mature (Reist and Bond 1988), so the ratio of spawners to nonspawners was expected to be on the order of 1:1 or 1:2 if the two groups mixed proportionally in the Innoko River.

In 2007, candidate fish were captured in the Upper Innoko River between Hather Creek and the Dishna River (Figure 2) using constantly monitored gillnets and hook-and-line angling methods. In 2008 and 2009, candidate fish were captured in the Innoko River upstream of Shageluk Slough (a waterway connecting the Yukon and Innoko rivers approximately 30 km upstream of Shageluk). This capture site is located approximately 85 km downstream of the radio tracking station on the Innoko River.

A total of 115 uniquely coded radio transmitters operating on three frequencies in the 162 MHz band were surgically implanted in inconnu using methods considered to be appropriate and effective for salmonid fishes (Winter 1996; Wagner et al. 2000; Jepsen et al. 2002). Transmitters weighed 26 g in air and were 73 mm long, 16 mm in diameter, and trailed a whip antenna 42 cm in length. They were programmed to transmit 24 hours a day from May 1 to October 31 and to become dormant from November 1 to April 30, permitting several years of tracking through the summer feeding and fall spawning seasons.

Following capture, inconnu were placed in an anesthetic bath. During 2007, we used the experimental anesthetic, Aqui-S®, at a concentration of 30 $mg{\cdot}L^{-1}$, which was an effective concentration for inconnu consistent with the experimental findings of Stehly and Gingerich (1999), Iversen et al. (2003), and Bowker et al. (2006). The experimental use of Aqui-S® was administered by the U.S. Fish and Wildlife Service under their Investigational New Animal Drug program (INAD 10-541-07-26). In spring 2008, the Food and Drug Administration halted the experimental use of Aqui-S® because high-dose, long-term exposure (two years) was found to cause cancer in male mice (National Toxicology Program 2010). During 2008 and 2009, a clove oil anesthetic solution was used at a concentration of 30 mg•L^{-1}. In the absence of an FDA approved immediate release anesthetic for fish, clove oil was selected because it is an effective anesthetic for salmonid fishes (Anderson et al. 1997; Woody et al. 2002) and is an approved food product for humans so there was no risk to people who might consume a tagged fish following release.

Anesthetized fish were placed in a V-shaped cradle and water was delivered to their gills during surgery. An incision approximately 3 cm in length was made through the body wall into the peritoneum anterior to the pelvic girdle and just to the fish's left of center to avoid centrally located blood vessels and nerve channels, as suggested by Winter (1996). The antenna was routed through a hole posterior to the pelvic girdle with a hypodermic needle and a grooved director in a modified, shielded-needle procedure (Ross and Kleiner 1982). The transmitter was placed into the peritoneum anterior to the pelvic girdle and the incision was closed with three monofilament sutures using a simple interrupted suture pattern (Wagner et al. 2000). Following surgery, fish were held in a recovery tote of fresh water and released when they were able to swim away vigorously.

To monitor passage of radio-tagged inconnu at critical drainage junctures, a total of four fixed-location, data-logging, radio receiving stations were established (Figure 1). These stations were situated on the Innoko River upstream of the primary tagging site and downstream of potential spawning areas, and downstream of spawning areas in the Koyukuk, Tanana, and Yukon River drainages. Data were collected during fall 2007 from the station on the Lower Innoko River, and from all of the stations during summer/fall 2008 through 2012.

Radio tagged inconnu were also located during the fall spawning season with a series of aerial survey flights over the identified spawning areas: Nowitna (Sulukna River), Koyukuk (Koyukuk mainstem and Alatna River), Tanana (Chatanika River and the Tanana River between Fairbanks and Delta), the Yukon Flats (mouth Chandalar River upstream to Circle), and over the Innoko River upstream from tagging sites. During aerial surveys, radio-tagged fish were identified based on unique electronic codes. Multiple records of each fish were recorded as the aircraft flew over and our best estimate of the actual location was based on the record with the greatest signal strength, which was thought to be within 1 km of the fish's actual location (Brown 2006).

Migration speeds for fish traveling upstream to spawning areas were calculated as the distance between the Innoko River station and either the Koyukuk or Yukon River station divided by the total time elapsed in days between the last record of a fish passing the Innoko station and the first record of the fish passing either the Koyukuk or Yukon River station. Post-spawning (downstream) migration rates were calculated based on the last observed time and position of a fish moving downstream following spawning during aerial tracking flights and the fish's arrival at the nearest tracking station.

Annual survival rates for mature inconnu were estimated from historical age data as a means to understand how many radio-tagged inconnu could be expected to survive during the second, third, fourth, and fifth years of the project. We used a catch curve procedure outlined by Robson and Chapman (1961) with 266 ages from the Yukon Flats spawning population randomly collected during the 1997 spawning migration (Figure 3; data from Brown 2000). Catch curve estimates of annual survival are valid if there is a reasonable assumption that recruitment to the sampled population, in this case the spawning population, is relatively consistent from year to year. Because our age distribution histogram did not suggest missing age classes or erratic recruitment, and the form was a reasonably smooth, log-normal distribution with a mode at 10 years, we considered it to be adequate for these exploratory purposes. Using these data and this procedure (Robson and Chapman 1961), we estimated annual survival of mature inconnu from the Yukon Flats spawning population to be 0.63 (95% CI = 0.59 to 0.68). Assuming this value is reasonable for the Yukon Flats population, and that other Yukon River populations experience similar mortality, approximately 37% of our tagged sample would be expected to perish each year. We reasoned that if we started with 115 fish, deployed as described between 2007 and 2009, and we calculated a depletion function at an annual rate of 0.37, we would see approximately 28 fish still alive in fall 2011. To empirically test our prediction we tracked our sample of radio-tagged inconnu for evidence of survival through 2011. Evidence of survival included records of migration past receiving stations, aerial survey locations demonstrating migration during the summer or fall, and harvest reports indicating that a fish had been alive. While some radio-tagged inconnu were reported harvested, the fates of other fish that we failed to detect were not known with certainty. We therefore examined annual survival of our radio-tagged sample in a qualitative manner, considering our results to be minimum estimates.

All data including individual fish lengths, sex (if available), transmitter frequencies and codes, location of tagging, and subsequent relocations by tracking station and aerial flights were entered into computer worksheets and are archived as *Innoko Inconnu Telemetry Data.xls*.

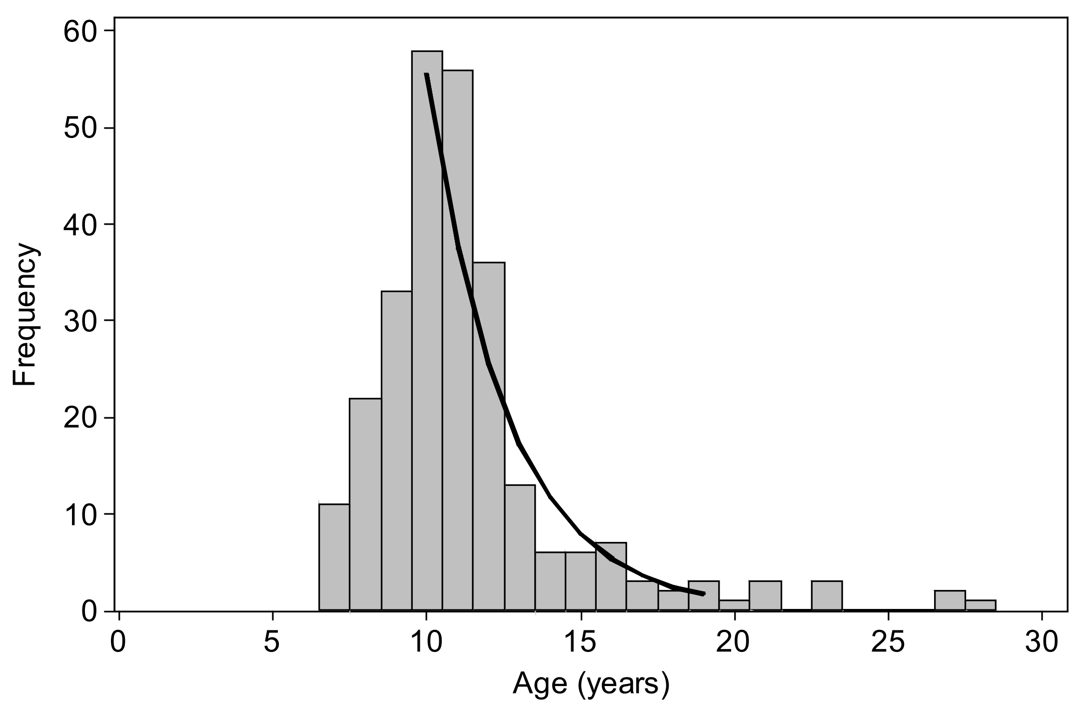

Figure 3.–Age frequency histogram of 266 mature inconnu from the Yukon Flats spawning population that were sampled at Rampart Rapids in 1997 (data from Brown 2000). A catch curve estimate of annual survival was calculated from the declining limb of the curve between the ages of 10 (T_0) and 19 (T_9) years, as illustrated with the line (Robson and Chapman 1961).

RESULTS

Radio transmitters were surgically implanted into a total of 115 mature size inconnu. Eighteen inconnu were fitted with radio transmitters during summer 2007. In June 2008 and 2009, 75 and 22 inconnu were radio-tagged (Table 1). The inconnu in this sample ranged from 64 to 97 cm FL with a mean of 78.9 cm (Figure 4).

Table 1.–Spawning origins of inconnu radio-tagged in the Innoko River drainage including the tagging year or group, number of fish tagged, known spawning destinations of fish, and number of fish for which spawning destinations were not obtained. The sum of known and unknown origin fish totaled 117, two fish more than were tagged, because two individuals migrated to both the Yukon Flats and Alatna River spawning areas and were thus double counted. The bottom row identifies the total number of fish in the sample with known spawning origins and their proportional distribution among the four spawning destinations observed in this study.

Tagging group	Number tagged	Yukon Flats	Alatna River	Sulukna River	Innoko River	Unknown origin
2007	18	4	1	0	4	9
2008	75	30	12	1	8	25
2009	22	11	2	1	5	4
Total	115	45	15	2	17[a]	38
Spawners	77	0.58	0.19	0.03	0.22	

[a] The Innoko River spawning area was discovered in fall 2010. Nine inconnu were identified in the spawning area in fall 2010 and 2011. Distinctive migration patterns into and out of the Innoko River during the 2007, 2008, and 2009 seasons indicated another eight fish in our sample were spawning in the Innoko River. We included them in this table.

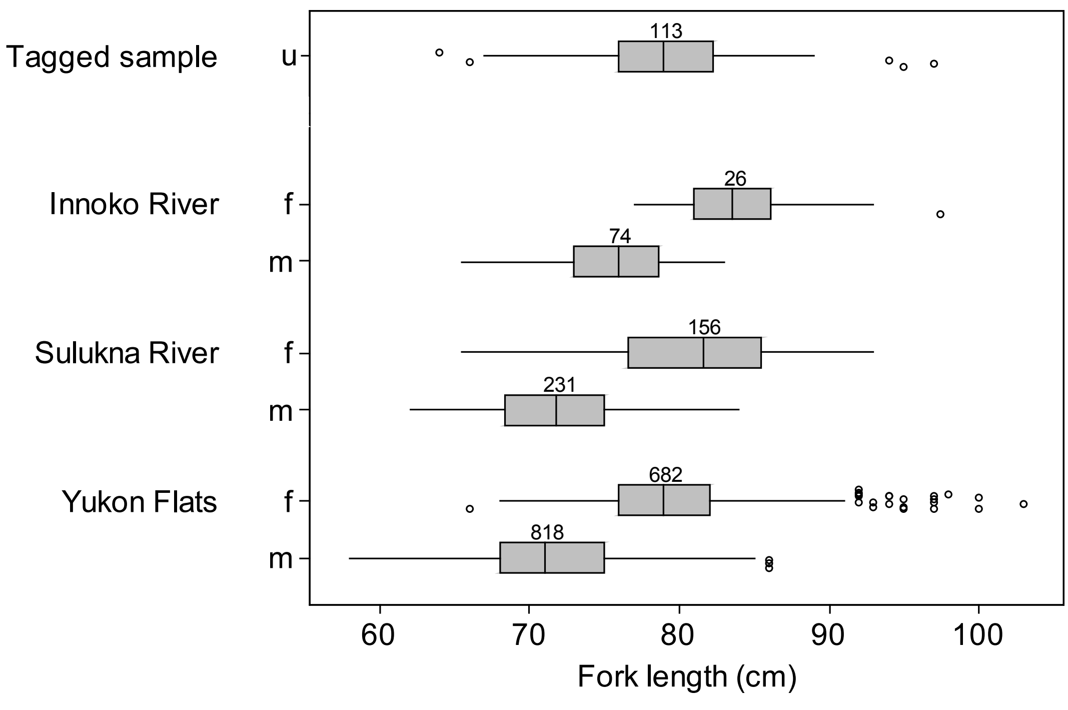

Figure 4.–Length distributions of radio-tagged inconnu, which were not identified to sex (u) because they were tagged in the spring and early summer when sexual characteristics were not apparent, and for female (f) and male (m) inconnu collected on or near the spawning locations of the Innoko River (this study), Sulukna River (Esse 2011), and Yukon Flats (Brown et al. 2012) populations. Sample sizes are indicated for each group.

SPAWNING ORIGINS

Tracking flights conducted just prior to and during the spawning seasons in 2007 through 2011 in combination with information from stationary receiving stations revealed that 77 of the 115 inconnu tagged in the Innoko River migrated to spawn in four spawning sites in the Yukon drainage (Table 1; Figure 5). Spawning origins were not identified for 38 of the radio-tagged fish; 3 were harvested and reported, 26 were presumed dead because they were not encountered during aerial surveys or in station records for two or more years following tagging, and 9 were regularly identified migrating past the Innoko River station during summer but did not migrate to upstream destinations to spawn during the course of the project.

Forty-five of the 77 radio-tagged inconnu with known spawning origins (58%) were located in the Yukon Flats spawning area. A total of 15 (19%) were found in the Alatna River site and there was no evidence that radio-tagged fish stopped to spawn in the Koyukuk River site.

Only two (3%) radio-tagged inconnu were located in the Sulukna River spawning area in the Nowitna River drainage.

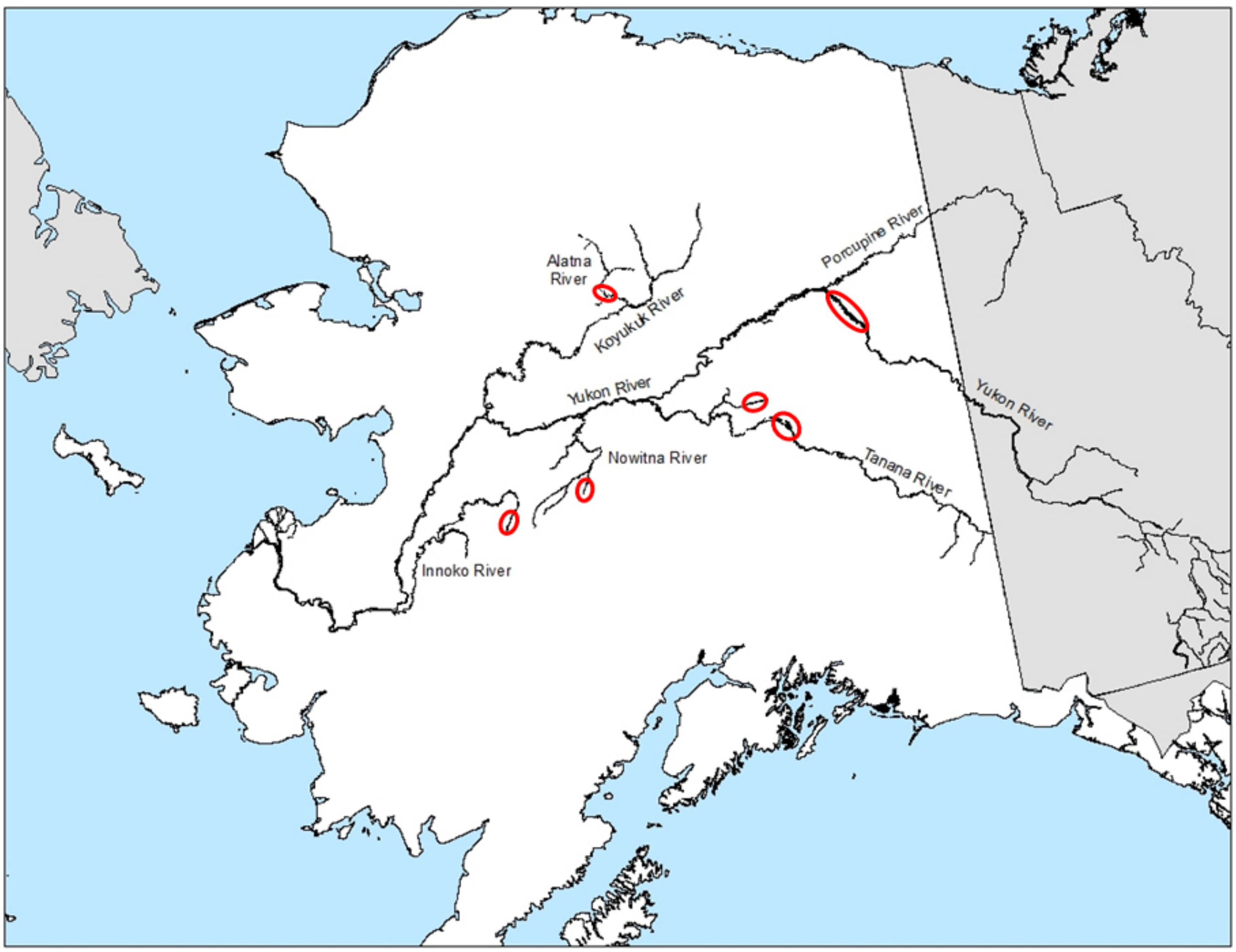

Figure 5.–The Yukon River drainage in Alaska and Yukon Territory with major tributaries labeled and elipses indicating the geographic locations of the six inconnu spawning areas that have been identified or verified with recent radiotelemetry and sampling data from this and other similar studies.

In fall 2010, a new spawning site was identified in the Upper Innoko River drainage during a tracking flight based on the presence of six radio-tagged inconnu within a short reach of the stream (Figure 5). In mid-September 2011, we visited the site and verified that a spawning aggregation was present. We captured 100 inconnu using angling methods, sacrificed seven females to verify spawning readiness with a gonadosomatic index [(egg weight • whole body weight^{-1}) • 100], verified that milt could be expressed from males, measured their lengths (FL), and collected 100 genetic samples. Gonadosomatic index values of the seven females ranged from 16 to 22, which was consistent with an inconnu preparing to spawn. Females in this sample (n = 26) ranged from 77 to 98 cm FL with a mean of 84 cm. Males in the sample (n = 76) ranged from 66 to 83 cm FL with a mean of 76 cm (Figure 4). Tracking records indicated that 17 (22%) of the inconnu radio-tagged in the Innoko River during the course of this study spawned in this newly identified spawning area.

Two inconnu were located by radiotelemetry in different spawning areas in subsequent years. One was detected in the Yukon Flats spawning area October 8 and 15, 2009 and subsequently was located on the Alatna spawning area on October 8, 2010. The other fish was detected on the Alatna River within the spawning area in September 27 and 29, 2008 and then at the Yukon Flats on October 8 and 17, 2009.

Spawning Frequency

Spawning frequency patterns of radio-tagged inconnu that were located in spawning areas during the five years of this study are listed in Table 2. Twenty-nine of the 115 individual radio-tagged fish were either never located following tagging or were harvested and provided no information of spawning pattern. Nine (10%) of the remaining fish were alive but did not migrate to spawning habitats during the study. Thirty-three (38%) spawned (migrated to spawning habitats) only one year. A total of 29 (34%) spawned in two years, 12 (14%) of which spawned in two consecutive years. Ten (12%) were located in spawning habitats during three years and seven of these (8%) spawned in three consecutive years. Five (6%) of the inconnu spawned in four consecutive years. Twenty-seven (31%) of the radio-tagged inconnu for which data are available spawned in two or more consecutive years.

Migration Timing

Records from radio receiving stations together with supplemental data from aerial surveys were combined to describe the timing and patterns of annual migration of inconnu. Specific migration patterns and the number of individual inconnu for which these patterns were consistent are diagramed in Figure 6. Inconnu migrated upriver past the Innoko River station, presumably to feed, beginning in late May with upriver migrations continuing through June. Inconnu that left the Innoko and subsequently were located in the Alatna River or Yukon Flats spawning areas were recorded migrating downstream past the Innoko station during late July and August. Fish migrating to the Alatna River spawning area entered the Koyukuk River over a relatively extended period of time encompassing July and most of August. Inconnu migrating to the Yukon Flats spawning area were recorded passing the Yukon River station during a relatively brief time period from late August through September, which is consistent with migration timing data from the Rampart Rapids test fish wheel as determined with daily catch rates (Brown et al. 2012). Post-spawning migrations of inconnu from the Upper Innoko, Alatna, and Yukon Flats spawning areas were relatively brief events occurring during mid-to-late October. Inconnu identified as non-spawning fish feeding in the Innoko River during summer, exited the Innoko River over an extended period of time from August through October.

Table 2.–Spawning patterns observed in radio-tagged inconnu during five years of data collection. Entries of "no," indicating that a fish was known to be alive but did not migrate to spawning habitats, and "yes," indicating that a fish migrated to spawning habitats, illustrate the different patterns of spawning that were observed. Blank cells indicate that fish failed to migrate past radio receiving stations and were not observed during aerial survey flights from that point on. Twenty-nine individuals were either never located following tagging or were harvested and provided no data on spawning patterns. The frequency column displays the number of radio-tagged fish that followed a particular pattern.

Tagging year	Second year	Third year	Fourth year	Fifth year	Frequency
no data					29
no					5
no	no				2
no	no	no	no		2
no	no	no	yes		1
no	no	yes	yes		1
no	yes				8
no	yes	no			3
no	yes	no	no		1
no	yes	no	yes		3
no	yes	yes			1
no	yes	yes	no	no	1
no	yes	yes	yes		1
no	yes	yes	yes	no	1
yes					20
yes	no	no	yes		2
yes	no	yes			12
yes	yes				7
yes	yes	no			2
yes	yes	no	yes		3
yes	yes	yes			4
yes	yes	yes	no		1
yes	yes	yes	yes		5

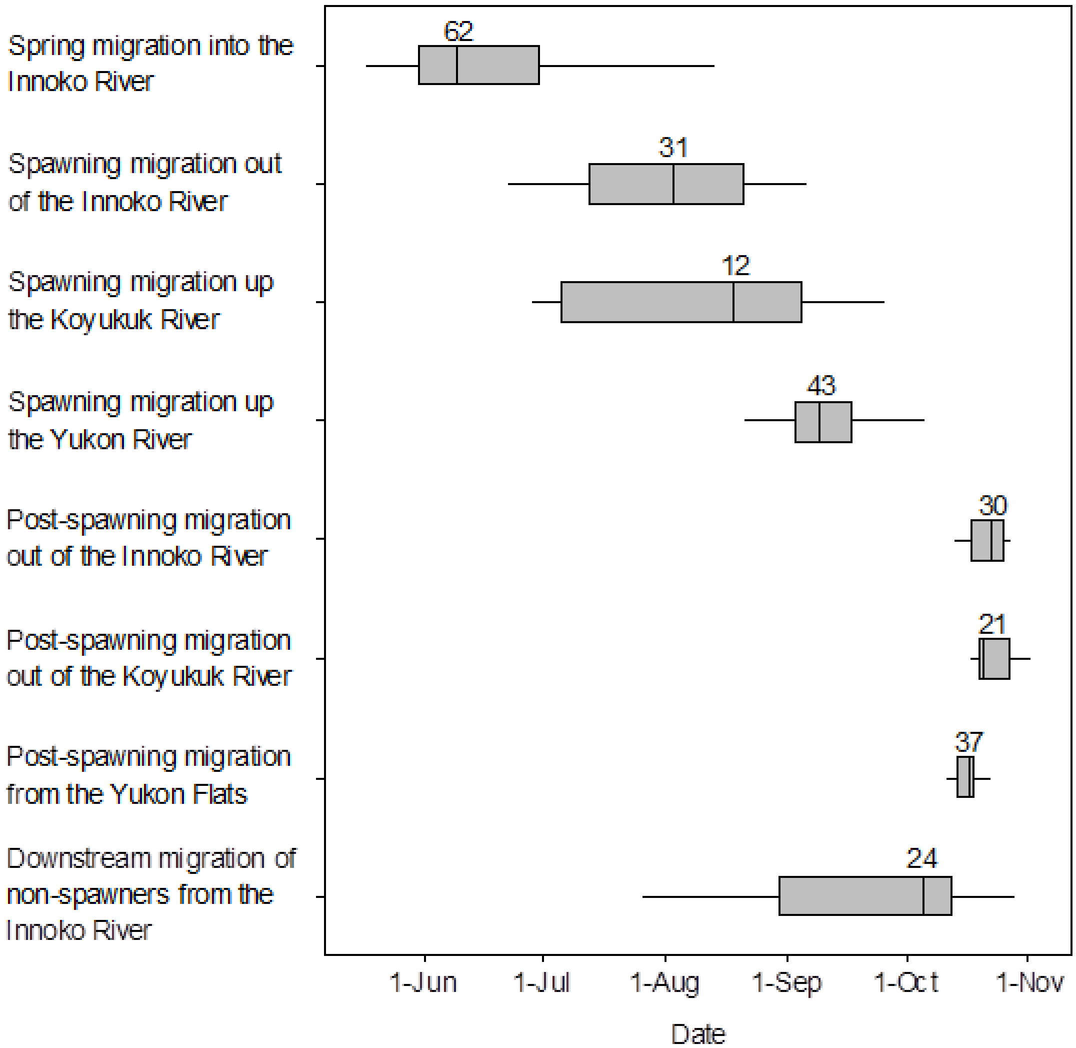

Figure 6.–Seasonal migration timing of radio-tagged inconnu based primarily on radio receiving station records along with some aerial survey data. Inconnu migrate into the Innoko River to feed during late May and June. Inconnu that leave the Innoko and subsequently migrate upstream to spawn in the Alatna River or Yukon Flats spawning areas tend to leave the Innoko River during late July and August. Fish migrating to the Alatna River spawning area enter the Koyukuk River over a relatively extended period of time encompassing July and most of August. Fish migrating to the Yukon Flats spawning area pass the Yukon River station during a relatively brief time period in September. Post-spawning migrations of inconnu from the Upper Innoko, Alatna, and Yukon Flats spawning areas were relatively brief events during mid-to-late October. Inconnu identified as non-spawning fish feeding in the Innoko River during summer, exited the Innoko River over an extended period of time from August through October.

MIGRATION SPEED

Migration speeds for 27 inconnu leaving the Innoko River and migrating to spawn in the Alatna or Yukon Flats spawning area ranged from 8 to 49 km/day with a median travel rate of 21 km/day (Figure 7). Following spawning, records from 40 fish traveling downstream toward overwintering habitat ranged from 12 to 129 km/day with a median rate of 55 km/day. Migration speeds were calculated for pre- and post-spawning fish only; necessary data for calculating migration speeds of non-spawning fish were not available.

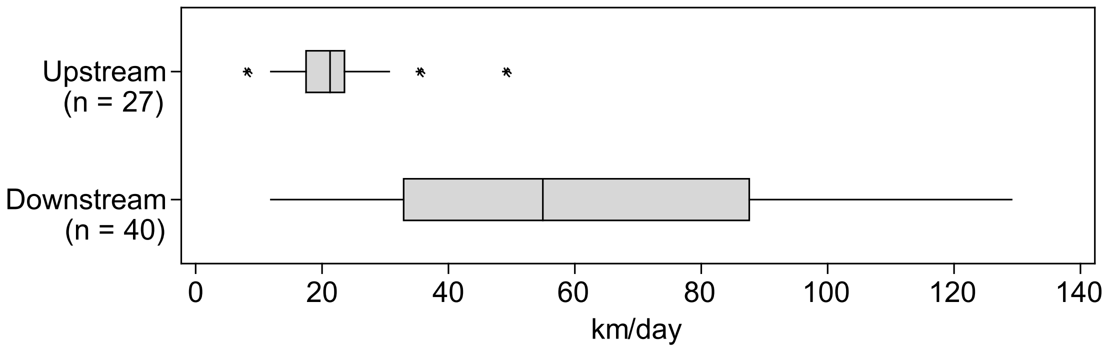

Figure 7.–Migration speeds of radio-tagged inconnu along the Yukon River and its tributaries as fish travel from the Innoko River feeding habitats to upstream spawning sites in the fall (median = 21 km/day), and to downstream overwintering habitats in the Lower Yukon River following spawning (median = 55 km/day).

ANNUAL SURVIVAL OF RADIO-TAGGED INCONNU

Overall annual survival of our radio-tagged inconnu appeared to be similar to our catch curve estimates using the 1997 age data from the Yukon Flats spawning population (0.63; 95% CI = 0.59 to 0.68), as described in the methods above. Annual survival estimates based on the number of living radio tagged fish from the annual collections ranged from 0.40 to 0.91 (n = 9) and averaged 0.67. The average was within the 95% CI of the catch curve estimate. Annual survival estimates within the tagging-year groups suffer low sample sizes and relatively large variation. When the tagging-year groups were combined and we considered just the two years following tagging that all three tagging years contributed to (T_1 and T_2), the annual sample sizes increased and annual survival estimates ranged across a narrower interval, from 0.57 to 0.72 (Table 3). Annual survival of these two annual samples averaged 0.65, again within the 95% CI of the catch curve estimate. The sum of tagged fish known to be alive in 2011 was 30, just two more than the 28 we expected based on our depletion calculation. Together, these data provide substantial support for an annual survival rate of mature Yukon River inconnu in the 0.60 to 0.70 range.

Table 3.–Annual survival estimates of radio-tagged inconnu for the three tagging years individually and combined. Data are organized in rows by tagging year and in columns for years T_0 (the tagging year) through T_n (n = the years elapsed following tagging) and mean annual survival estimates (*s*) from the tagging years and combined samples. All tagging years were able to contribute three annual samples, which allowed two annual survival estimates with all tagged fish. These data include the number of tagged fish known to be alive in year T_n, and in parentheses, the proportion that survived the previous year, which is our empirical estimate of *s*.

Year	T_0	T_1	T_2	T_3	T_4	Mean *s*
2007	18 (1.00)	14 (0.78)	11 (0.79)	10 (0.91)	4 (0.40)	0.72
2008	75 (1.00)	38 (0.51)	26 (0.68)	16 (0.62)		0.60
2009	22 (1.00)	13 (0.59)	10 (0.77)			0.68
Combined	115 (1.00)	65 (0.57)	47 (0.72)			0.65

DISCUSSION

Spawning origins were identified for 77 inconnu radio-tagged in the Innoko River drainage during the course of this study. Forty-five (58%) migrated into the Yukon Flats, 15 (19%) into the Alatna River, 2 (3%) into the Sulukna River, and 17 (22%) into the Upper Innoko River (Table 1). The percentages sum to more than 100% because two fish migrated to both the Yukon Flats and Alatna River spawning areas and are counted as members of both. All radio-tagged inconnu from the Innoko drainage that migrated into the Koyukuk drainage and were present during the fall spawning period traveled to the Alatna River as their farthest upstream destination. Two fish migrated into the Koyukuk River during summer, presumably to forage in the drainage, and then exited and spawned in the Yukon Flats later in the fall. There was no indication of spawning in the Koyukuk River mainstem, a putative spawning area identified by Alt (1969, 1970) based on capture data and visual aerial surveys. Our telemetry data suggests that there is a single spawning area in the Koyukuk River drainage located in the Alatna River.

A separate but similar inconnu radio-tagging study is currently operating in the Tanana River. Results from that study verified that the Chatanika River spawning area is still being used by at least a small number of inconnu (A. Gryska, ADF&G, pers. com.). In addition, a new spawning area was identified in the mainstem Tanana River in a heavily braided reach between the mouths of the Chena and Salcha rivers. None of the inconnu tagged in the Innoko River were located in the Chatanika or Tanana River spawning areas. One radio-tagged inconnu from the Innoko migrated into the Tanana drainage during summer 2011, presumably to feed, but was not detected during aerial surveys of spawning areas in the fall. These data suggest that few, if any, inconnu from the Tanana River populations use the Innoko River as feeding habitat, or that the Tanana River populations are less abundant than other populations in the drainage, thereby reducing the probability of capturing Tanana inconnu while they are feeding amongst members of other populations in the Innoko River during the summer months.

The probability of anadromy appears to vary for the different inconnu populations within the Yukon River drainage. Brown et al. (2007), identified elevated otolith strontium levels indicating anadromy in only 2 of 10 inconnu sampled from the Tanana River compared to 12 of 12 inconnu sampled from the Yukon Flats population and 8 of 10 inconnu sampled from the

Alatna River population. Using similar sampling and otolith chemistry techniques, Esse (2011) found evidence of anadromy in 3 of 12 inconnu from the Sulukna River spawning population. These studies were designed to detect anadromy not to estimate the anadromous proportion within the sampled populations, but their data support the concept that anadromy is more common in the Yukon Flats and Alatna River populations than in the Tanana and Sulukna River populations. If this is true, we might expect a smaller fraction of the Tanana and Sulukna River spawning populations to migrate into the Lower Yukon River than from the Yukon Flats and Alatna River populations.

The probability of sampling an inconnu foraging in the Innoko River that has spawning origins far upstream in the Yukon River drainage must be a function of both relative abundance of the contributing spawning populations and the probability of anadromy within those populations. As discussed above, the probability of anadromy within the upstream spawning populations appears to be relatively high for the Yukon Flats and Alatna River populations and relatively low for the Tanana and Sulukna River populations (Brown et al. 2007; Esse 2011). As a result, our ability to estimate relative population sizes based on the identified spawning origins of radio-tagged fish cannot be applied uniformly across all populations. The Yukon Flats and Alatna River spawning populations appear to exhibit similarly high probabilities of anadromy (Brown et al. 2007). If the choice to migrate into the Innoko River is a random process for foraging inconnu in the Lower Yukon River, similar proportions of those populations would be expected to enter the drainage. The relative difference in our radio-tagged sample among the Yukon Flats and Alatna River spawning locations, 58:19 or approximately 3:1, is probably a good estimate of relative spawning population abundances. The proportion of tagged inconnu that migrated into the Sulukna River spawning site (approximately 3% of fish with known spawning origins) probably underestimated the relative abundance of that spawning population because a smaller fraction would be expected to migrate to the Lower Yukon River drainage and forage in the Innoko River. In an opposite manner, the proportion of tagged inconnu that migrated into the Innoko River spawning site (approximately 22% of fish with known spawning origins) probably overestimated relative abundance because all members would be expected in the Innoko River.

A new inconnu spawning area was identified in the Innoko River drainage during this study (Figure 5). This site was first discovered in 2010 when six radio-tagged inconnu were located within a 2 km reach in the Upper Innoko River that had previously been identified as a humpback whitefish *Coregonus pidschian* and least cisco *C. sardinella* spawning area (Alt 1983). Inconnu were sampled by personnel who traveled by boat to the site in September 2011. Boat and aerial surveys revealed that six radio-tagged fish were present (three repeat spawners from 2010) during the late September, early October spawning period. Distinctive migration patterns into and out of the Innoko River during the 2007, 2008, and 2009 seasons, as recorded on the station in the lower river, together with aerial tracking information indicated that at least eight additional radio-tagged fish in our sample were spawning in the Innoko River. Based on these data, 17 inconnu from our sample, 22% of fish with known spawning origins, were members of the Innoko River spawning population (Table 1).

It has always been assumed that inconnu exhibit spawning site fidelity. Evidence to support this assumption is based primarily on tagging and genetics evidence from northwest Alaska, where there are two inconnu spawning populations, one in the Upper Kobuk River and the other in the Upper Selawik River (Alt 1969). During the mid-1990s there were several annual mark and recapture tagging operations designed to estimate abundance of both spawning populations

(Taube and Wuttig 1998; Underwood et al. 2000). Thousands of fish were tagged in upstream reaches of both drainages and during subsequent years there were 43 recaptures in the Kobuk River spawning reach and 35 recaptures in the Selawik River spawning reach, but none had switched drainages. A genetics analysis of restriction fragment length polymorphisms in mtDNA and nucDNA concluded that there was very little gene flow between the two populations (Miller et al. 1998). Nearly all inconnu tagged in the Innoko River study that spawned more than once demonstrated fidelity to a single spawning site. However, we documented two instances in which individual fish spawned during consecutive years in different sites. In one case the fish spawned first in the Yukon Flats and the next year in the Alatna River, and in the second case the fish spawned first in the Alatna River and the next year in the Yukon Flats. The Alatna River and Yukon Flats spawning areas are separated by more than 1,500 km along different branches of the river suggesting that the two fish exhibiting infidelity had chosen a different fork of the river hundreds of km downstream from spawning areas and followed individuals from the other spawning population rather than sensing the spawning habitat. Because the Yukon River is turbid during late summer and fall (Brabets et al. 2000) and the Koyukuk River is tundra stained and can be turbid, we have to assume that the smell of other pre-spawning inconnu rather than sight guided the fish to the spawning areas. We know of only one other instance where straying by inconnu between spawning areas has been reported. Stuby (*in prep*) noted that two inconnu were found in spawning areas in adjacent branches of the Middle Fork Kuskokwim River, the Big River and the mainstem Middle Fork. Similar to our thoughts on the mechanism of straying to new spawning sites in the Yukon River drainage, Stuby (*in prep*) suggested that inconnu migrating to spawn in the two forks of the Middle Fork Kuskokwim River may have followed other pre-spawning inconnu into an adjacent tributary.

Estimating annual survival of a highly migratory species within a large river system is a challenging prospect. Our initial interest in pursuing annual survival was to predict the number of radio tags that could be active several years after tagging as a means of project planning. The catch curve estimates of survival, despite the uncertainties inherent with that procedure, made it clear that even with very long duration transmitters, the project would be forced to expire because our sample of radio-tagged fish would quickly become too small to warrant the expense of tracking them through the drainage. The fact that our empirical survival estimates (Table 3) were so similar to the catch curve estimates from the age data, and that the predicted number of living radio-tagged fish for the time interval (28) was so close to what we observed (30), suggests that annual survival of mature inconnu in the Yukon River drainage is relatively consistent among populations and over time. Perhaps the probability of capture in gillnets and fish wheels during long spawning migrations is relatively constant and keeps inconnu populations stable. Despite the empirical support for the calculated values of annual survival, there are weak elements in our ability to determine fates for radio-tagged inconnu in the large river environment. We are confident in our assessment of the fish we classified as "living," but suspect that a small number of those we did not classify as living may actually be alive and occupying habitats that were not surveyed or monitored. We therefore consider our empirical estimates of annual survival to be minimums.

It has usually been assumed that northern coregonid populations were not capable of spawning during two successive years (Alt 1969; Reist and Bond 1988; Lambert and Dodson 1990). Lambert and Dodson (1990) examined the annual energetic requirements for spawning lake whitefish *C. clupeaformis* and cisco *C. artedii* populations in a river in southern Hudson Bay and concluded that they could not obtain enough nutrition to spawn two years in succession and had to skip spawning for at least 1 year after each year in which they spawned. Evidence for the occurrence of skip spawning of individual fish is strong for most coregonid species. Alt (1969), for example, observed two stages of gonad development in mature female inconnu in northwest Alaska during summer and concluded that those with larger eggs would spawn that year and those with smaller eggs would not. Brown (2004) plotted gonadosomatic index (GSI) values against age and size from a sample of 30 female broad whitefish captured in September in the Selawik River delta in northwest Alaska. He showed that approximately half of the sample that were older and larger than minimum age and length at maturity had low GSI values (<3%) and would not spawn that fall. Moulton et al. (1997) used similar data to argue that approximately half of the mature humpback whitefish and least cisco sampled in Dease Inlet in northern Alaska would not spawn that fall. Despite the sampling evidence that some mature whitefish of most species skip spawning some years, the prevalence of skip spawning in populations or through the lifetime of individual fish is largely speculative.

Annual or sequential year spawning of inconnu has been documented with tagging studies in spawning reaches. For example, in northwest Alaska, numerous spawning inconnu with anchor tags were located in upstream spawning reaches of the Kobuk (Taube and Wuttig 1998) and Selawik (Underwood 2000; Hander et al. 2008) rivers during two consecutive spawning seasons. Similar to the anchor tag evidence, 9 of 26 spawning inconnu equipped with radio tags in the Selawik River were present in the spawning reach during two consecutive spawning seasons (Hander et al. 2008). Inferring annual spawning for inconnu based on a fish's presence in a spawning area during spawning time requires sampling evidence that only spawning inconnu are present. Alt (1969), who sampled Kobuk River inconnu in their spawning habitat, Brown (2000), who sampled the fall spawning migration of Yukon River inconnu downstream from their spawning habitat, Howland (1997), who sampled spawning migrations of inconnu in the Slave and Arctic Red rivers in the Mackenzie River drainage, and Esse (2011), who sampled pre- and post-spawning inconnu downstream from the Sulukna River spawning area, all reported that only fish preparing to spawn were present. These sampling studies support the assumption that a fish's presence in spawning habitat during spawning season indicates its intention to spawn.

Spawning frequency patterns of inconnu in this study (Table 2) were highly variable, with some fish spawning once in three or four years and others engaging in 1,000 km or more spawning migrations three or four years in a row. In an analogous radiotelemetry study on the Kuskokwim River, Stuby (2010, *in prep*) reported sequential spawning for inconnu with a similar mix of frequent and infrequent spawners. In a more directed radiotelemetry study on the Kobuk River in northwest Alaska, Savereide (2010) found that a substantial fraction of both male and female inconnu tagged during fall spawning migrations in the Kobuk River returned to spawn in consecutive years (Savereide 2010). These data indicate that sequential year spawning is not rare, although it is also not possible to characterize a spawning frequency pattern for a population. If we assume that spawning takes place when sufficient resources are accumulated to support the cost of migration and production of gametes, then the observed high variability in spawning frequency among individuals indicates that some inconnu are very effective at foraging while others apparently are not.

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