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ARTICLE

Distribution, Stock Composition and Timing, and Tagging Response of Wild Chinook Salmon Returning to a Large, Free-Flowing River Basin

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Abstract
Chinook Salmon *Oncorhynchus tshawytscha* returns to the Yukon River basin have declined dramatically since the late 1990s, and detailed information on the spawning distribution, stock structure, and stock timing is needed to better manage the run and facilitate conservation efforts. A total of 2,860 fish were radio-tagged in the lower basin during 2002–2004 and tracked upriver. Fish traveled to spawning areas throughout the basin, ranging from several hundred to over 3,000 km from the tagging site. Similar distribution patterns were observed across years, suggesting that the major components of the run were identified. Daily and seasonal composition estimates were calculated for the component stocks. The run was dominated by two regional components comprising over 70% of the return. Substantially fewer fish returned to other areas, ranging from 2% to 9% of the return, but their collective contribution was appreciable. Most regional components consisted of several principal stocks and a number of small, spatially isolated populations. Regional and stock composition estimates were similar across years even though differences in run abundance were reported, suggesting that the differences in abundance were not related to regional or stock-specific variability. Run timing was relatively compressed compared with that in rivers in the southern portion of the species' range. Most stocks passed through the lower river over a 6-week period, ranging in duration from 16 to 38 d. Run timing was similar for middle- and upper-basin stocks, limiting the use of timing information for management. The lower-basin stocks were primarily later-run fish. Although differences were observed, there was general agreement between our composition and timing estimates and those from other assessment projects within the basin, suggesting that the telemetry-based estimates provided a plausible approximation of the return. However, the short duration of the run, complex stock structure, and similar stock timing complicate management of Yukon River returns.

Chinook Salmon *Oncorhynchus tshawytscha* spawn in rivers and streams throughout the northern Pacific Rim, ranging from small coastal drainages to vast river basins (Healey 1991; Heard et al. 2007). This species displays a wide range of life history strategies and behavioral forms, with returns often composed of multiple age-classes, complex population structures, and variable run timing. This diversity undoubtedly reflects the opportunities and constraints experienced by the

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fish during their spawning migration and after they reach their final destination. Information on the run characteristics of the returns provides numerous insights into the suitability of the conditions encountered and the physical capabilities of the fish. Increasingly, human activities and anthropogenic factors are impacting salmon populations in rivers throughout their range (National Research Council 1996; Lichatowich et al. 1999). Basic information on the spawning distribution, stock structure, and run timing is fundamental to understanding and managing Chinook Salmon returns and, when needed, to facilitate conservation efforts. However, obtaining this type of information is fairly challenging in large, free-flowing rivers, where the ability to access, sample, and evaluate the run is limited.

Large numbers of Chinook Salmon return to the Yukon River, a large, northern river basin in Alaska and northwestern Canada (Figure 1). The Yukon River is generally considered the fourth largest drainage in North America, exceeded in length only by the Mississippi, Missouri, and Mackenzie rivers. Although less numerous than other salmon species, Chinook Salmon support important commercial and subsistence fisheries throughout the basin and are an integral part of the Yukon River ecosystem. Because of the international nature of the drainage, the returns are jointly managed by the United States and Canada to maintain acceptable spawning escapements, support subsistence fisheries for local residents, and provide commercial and sportfishing opportunities when appropriate (Yukon River Salmon Act 2000). Management efforts are complicated by the complex stock structure and multiple age-classes of the return. These issues are exacerbated by the massive size and remote nature of the basin; difficulties associated with determining the stock-specific abundance, structure, and timing of the returns; the presence of other, temporally similar species of salmon (most notably summer Chum Salmon *O. keta*); and the need to equitably allocate harvests among numerous fisheries and user groups scattered throughout the basin.

Recent trends have further confounded management efforts. Yukon River Chinook Salmon returns were relatively stable until the late 1990s, when dramatic declines in abundance were reported (JTC 2001; Heard et al. 2007). This trend has continued during subsequent years and resulted in the closure or drastic reductions in commercial fisheries, severe restrictions on subsistence harvests, and difficulties in meeting

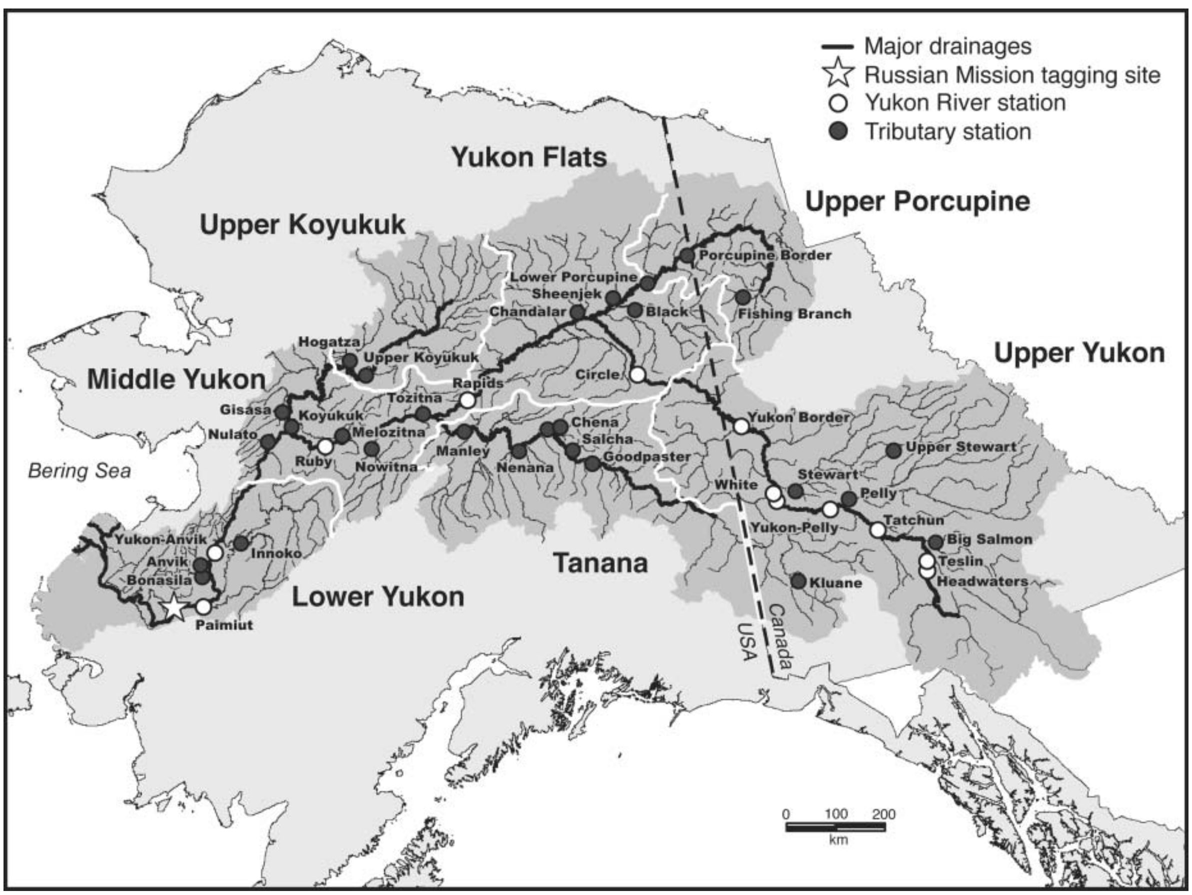

FIGURE 1. Map of the Yukon River basin showing the regional areas, major drainages, and locations of the lower-river tagging site near Russian Mission and the tracking stations on both the Yukon River main stem and associated tributaries.

regional and basinwide escapement goals (ENS 2012; JTC 2013). Annual harvests within the basin averaged 155,480 fish from 1961 to 1997, compared with less than 78,930 fish during 1998–2012 (based on data from JTC 2013). Just over 28,900 fish were harvested in 2012. Similar trends have been observed for Chinook Salmon in other large rivers in western Alaska (Heard et al. 2007). Possible reductions in fish size (JTC 2006) and shifts in the age composition to younger fish (based on data from Karpovich and Dubois 2007 and Schumann and Dubois 2012) have also been reported.

Various approaches have been used to determine the status of Chinook Salmon returns in the Yukon River basin, including test fisheries, enumeration weirs, counting towers, sonar counts, aerial surveys, and spawning ground sampling (JTC 2006; Hayes et al. 2008). Although informative, these methods either provide information specific to particular tributaries or stocks or generalized information about the entire run without reference to the different components. Developing technologies have made it possible to collect information on a more comprehensive scale. In recent years, genetic stock identification (GSI) sampling has been routinely used to estimate run composition and timing within the basin and in local fisheries (Smith et al. 2005; Decovitch and Howard 2011; Flannery et al. 2012). Similarly, advances in equipment and tracking capabilities have made it possible to use radiotelemetry to collect detailed information on salmon movements in large river drainages (Burger et al. 1985; Eiler et al. 1992; Hinch et al. 2002; Keefer et al. 2004). Unlike other sampling methods, telemetry makes it possible to repeatedly locate and identify large numbers of wide-ranging, highly mobile individuals even when water visibility is limited or when working in remote or inaccessible areas. This approach can provide progressive information on the upriver movements and status of the fish on both a stock-specific and basinwide scale.

In response to the declining abundance of Yukon River Chinook Salmon, a basinwide telemetry study was conducted during 2002–2004 to provide detailed information on the run characteristics of the return. Chinook Salmon were captured and radio-tagged in the lower basin and tracked upriver, with some fish traveling over 3,000 km from the tagging site. In this paper, we describe the upriver dispersal, spawning distribution, stock composition, and stock-specific timing of the return—information essential to ongoing conservation and management efforts—and discuss the implication of composition and timing patterns for Chinook Salmon returns in large river basins. Many large rivers with sizable Chinook Salmon runs are heavily regulated with controlled flows and impounded reaches, and the returns are frequently comprised of both wild and hatchery fish. In contrast, the Yukon River is relatively pristine and essentially free-flowing and the returns are composed almost exclusively of wild stocks, providing an opportunity to document and examine run characteristics under natural conditions. Because adverse effects from capture and handling can bias study results, we also examine and discuss the posttagging response exhibited by the fish.

METHODS

Study area.—The Yukon River basin drains a watershed of more than 855,000 km^2. The main river (hereafter referred to as the main stem) alone flows for more than 3,000 km from its headwaters in Canada to the Bering Sea (Figure 1). Several major tributaries flow into the main stem, including the Koyukuk and Tanana rivers in the United States; the Stewart, White, Pelly, and Teslin rivers in Canada; and the Porcupine River, which transects both countries. The basin also includes numerous medium and small tributaries. The basin is extremely remote, with access to most areas limited to boat or aircraft.

In addition to its immense size, the Yukon River is the fifth largest drainage in North America in terms of total annual discharge and exhibits considerable temporal variability, with greater flows during the summer months (Brabets et al. 2000; Yang et al. 2009). The river is relatively deep, with channel depths exceeding 20 m in the lower basin as opposed to 12–14 m downstream of the Yukon–Tanana River confluence and 5–7 m near the U.S.–Canada border (distances of ~1,100 and 2,000 km from the river's mouth, respectively). Most reaches of the basin consist of a primary river channel with occasional side channels and sloughs, although the main stem is extensively braided in the area commonly referred to as the Yukon Flats. Sections of the Tanana River, White River, and the Canadian main stem are also noticeably braided. Regional designations (Figure 1) were based on geographic location and the general geomorphology of the area (e.g., the lower reaches of the Porcupine River were considered part of the Yukon Flats due to similarities in landscape and river characteristics).

Although harvests have been severely restricted in recent years, Chinook Salmon are a major source of food in many remote communities and provide income for local residents. Subsistence and commercial fisheries occur throughout the basin, with most fishing effort concentrated near villages along the main stem (JTC 2013). Fish are also harvested in a number of tributaries, including the Koyukuk, Tanana, Chandalar, Porcupine, Stewart, Pelly, and Teslin rivers. Limited sportfishing takes place within the basin.

Fish capture and handling.—We captured adult Chinook Salmon with drift gill nets in the lower Yukon River near the village of Russian Mission (Figure 1). This site was selected because it (1) consisted of a relatively narrow, unbraided section of river, increasing the probability of capturing a representative sample, (2) was downriver of most known Chinook Salmon spawning areas (only a few small spawning populations have been reported farther downstream), and (3) was upriver of significant commercial and subsistence fisheries lower in the basin. During 2002, we also captured fish near the village of Marshall, located approximately 90 km downriver from Russian Mission. Local fishers were contracted to fish the area from early June to mid-July, with project personnel handling the fish and collecting data. Both day (0900–1700 hours) and night (1800–0200 hours) shifts were employed during the study.

The fish were caught with drift gill nets constructed with cable laid netting (no. 12 stretch mesh and 21.5 cm mesh size). The nets were 46 m long and 7.6 m deep and hung at a 2:1 ratio. This configuration was effective for capturing Chinook Salmon while minimizing Chum Salmon bycatch. The nets were monitored continually and the fish removed immediately after capture. The netting was cut to facilitate removal and minimize injuries. We used a dip net with soft, fine-mesh netting to lift fish into the boat for tagging. A maximum of two fish (the first two uninjured individuals encountered) were tagged per drift to minimize both handling time and potential sampling bias if the stocks of fish were poorly mixed. The remaining fish were released from the gill net while still in the river. Fish retained for tagging were placed in a neoprene-lined tagging cradle submerged in a tote of freshwater. A pump circulated river water into the tote while the fish were being processed. Anesthesia was not used during the procedure.

We tagged the fish with pulse-coded radio transmitters in the 150–151 MHz frequency range that were manufactured by Advanced Telemetry Systems (Isanti, Minnesota). The transmitters (5.4 cm long and 2.0 cm in diameter, with a 30-cm transmitting antenna, and weighing 20 g) were gently inserted through the mouth and into the stomach using a plastic tube 0.7 cm in diameter. Each transmitter emitted a unique signal based on a combination of frequency and signal pattern (as described by Eiler 2012), making it possible to identify individual fish. Transmitters were also equipped with a motion sensor and activity monitor similar to those described by Eiler (1990). The motion sensor inserted additional signal pulses into the signal burst each time the transmitter moved. The activity monitor changed the signal pattern to an inactive mode if the motion sensor was not triggered for 24 h; the signal reverted to the original pattern if the motion sensor was activated. Transmitters had a minimum battery life of 90 d. The fish were marked externally with spaghetti tags attached just below the dorsal fin (as described by Wydoski and Emery 1983) to help identify tagged individuals caught in fisheries or located in spawning areas.

We also collected information on the physical characteristics of the fish, including body length (mideye to fork of tail) and external color. Most references to changes in skin color by maturing Chinook Salmon are limited to general descriptions comparing the marine phase to fish in spawning condition (Scott and Crossman 1973; Mecklenburg et al. 2002), with few details on the transitional stages. To minimize subjectivity, our classification was based on the extreme color differences observed in the lower river: iridescent silver, silver, and blush (silver with reddish tinges). Iridescent silver indicated that the fish were not as advanced in their transition to freshwater as those with silver coloration; the initial onset of spawning coloration (blush) provided an external sign of advancing sexual maturation. A tissue sample was taken from the axillary process for GSI studies, and scales were collected to provide age data (as described by DeVries and Frie 1996). The sex of the fish was not recorded because of difficulties in accurately distinguishing sex in the lower river due to the lack of distinct external characteristics. We released the fish back into the main river immediately after the tagging procedure was completed. Handling, from removal of the net from the water to release, took about 6–8 min per fish.

Tracking procedures.—The fish that moved upriver were tracked with remote tracking stations (as described by Eiler 1995, 2012) placed at 40 sites throughout the basin (Figure 1). The sites were located on important migratory routes and major tributaries. The stations consisted of several integrated components, including a data-logging radio receiver (Advanced Telemetry Systems), satellite uplink (Campbell Scientific, Logan, Utah), and directional receiving antennas (Cushcraft, Starkville, Mississippi) oriented upriver and downriver to provide information on the general location of the fish in relation to the site. A self-contained power system (consisting of a bank of six 6-V, sealed lead-acid batteries connected in series and parallel (12 V, 610 ampere-hour) and charged by two 80-W solar panels) supplied continual power to the stations.

Fish within reception range were detected and identified by the stations. The receiver recorded the date and time a fish was present at the site, the signal strength of the transmitter, and the relative position of the fish (i.e., upriver or downriver from the station). This information was summarized and recorded at 10-min intervals and used to determine when the fish moved past the site. Occasionally fish were not detected by the stations, particularly at Paimiut, the Yukon–Anvik River confluence, and to a lesser extent at Ruby (comprising 24, 15, and 7% of the fish passing the site, respectively), presumably due to fish swimming at deeper depths; the depth of the main channel at these sites was 25, 16, and 14 m, respectively. These fish were subsequently recorded at stations farther upriver. Essentially all fish (99–100%) were recorded by stations near the Koyukuk River mouth (6-m depths), Manley (8-m depths), Rapids (10-m depths), and the other main-stem and tributary sites.

Because of the isolated nature of the sites, the data collected by the stations (including information on operational performance, e.g., the power levels of station components and whether the reference transmitter at the site was properly recorded) were transmitted every hour to a geostationary operational environmental satellite and relayed to a receiving station operated by the National Oceanic and Atmospheric Administration's National Environmental Satellite and Data Information Service near Washington, D.C. These data were accessed daily via the Internet and uploaded to a computerized database (Oracle, Redwood Shores, California) for analysis and entry into a geographical information system (GIS) mapping program (ArcMap, version 10.0; ESRI, Redlands, California) for spatial comparisons (Eiler and Masters 2000). The program flagged information that indicated problems with station operations so that corrective action could be taken and created daily summaries of the upriver movements of the fish.

Based on the information collected by the stations, periodic aerial surveys were conducted to locate fish between station sites in nonterminal areas (i.e., intermediate or transitional reaches of the drainage) and upriver of stations on terminal tributaries (i.e., bounded reaches of the drainage). Fish were tracked from fixed-wing aircraft and helicopters as described by Eiler (2012). Helicopters were also used to access remote areas to determine the status of the fish and recover transmitters. Tracking receivers equipped with an integrated Global Positioning System (GPS) receiver were used during the surveys to standardize the location records of the fish.

Assessing upriver movements.—The response of each fish to the capture and handling procedures was evaluated based on the resumption of upriver movements and the swimming behavior exhibited after release. Fish that passed Paimiut (the first station site, located approximately 62 km upriver from Russian Mission) were considered to have resumed upriver movements. Swimming behavior was assessed by comparing the migration rates (km/d) of the fish from their release site to Paimiut in relation to the distance traveled. The distance to Paimiut varied because we captured, tagged, and released the fish while drifting through the tagging area. Distances ranged from 29 to 94 km for fish tagged at Russian Mission and from 139 to 152 km for fish tagged at Marshall. Only fish traveling to terminal tributaries in the upper reaches of the basin (>700 km upriver from Paimiut) were included in this analysis to avoid confounding issues between swimming speed and proximity to spawning areas. Differences in migration rates between the first two sections of river traversed by the fish—from the release site to Paimiut and from Paimiut to the Yukon–Anvik River confluence (133 km upriver from Paimiut)—were also compared for these fish.

Station and aerial tracking data were systematically reviewed postseason to determine the final location of all tagged fish and to verify that the records reflected a sequential progression past the station sites. Fish tracked to terminal tributaries were deemed to have reached their final destination and were designated as members of the spawning stock associated with that tributary. The status of fish last located in nonterminal areas, such as reaches of the main stem, was less certain because these individuals could represent fish spawning in nearby areas or fish in-transit to spawning areas farther upriver. Many nonterminal areas were turbid and hard to access, making verification of spawning activity unfeasible. Although it was beyond the scope of this study to characterize spawning habitat, we used the GIS mapping program to compare the final locations of the fish with elevation and physiographic overlays of the basin (provided by U.S. Geological Survey [http://agdc.usfs.gov/data/usgs/water/yukon.html]). General river type (described by Rosgen 1994) was also noted for terminal tributaries.

We asked fishers within the basin to report any radio-tagged fish they caught. Several steps were taken to promote this cooperative effort, including a reward for the tags returned, regular presentations at fishery meetings, information flyers posted in local communities, and personal contacts with local fishers (which often had the most impact but were difficult to implement on a large scale). Fish were also considered to have been harvested if their transmitters were located out of the water in villages or fish camps during aerial surveys, even if the recovery was not reported.

Estimating stock composition.—Efforts to estimate stock composition were confounded by several factors. Returning Chinook Salmon passing through the lower Yukon River are composed of a number of distinct stocks that differ in magnitude and run timing, and the numbers of fish tagged daily were not always in proportion to run abundance. Varying proportions of tagged fish were also intercepted in fisheries before reaching their final destination. The naive assumption that stock composition was equal to the observed distribution of radio-tagged fish escaping to spawning areas was therefore rejected. Stock composition estimates in the lower river (i.e., near Russian Mission) were therefore based on the distribution of radio-tagged fish tagged per day, weighted by daily indices of abundance at the capture site, and adjusted to account for tagged fish removed in upriver fisheries (described below). This approach provided daily and seasonal estimates of the relative abundance of stocks passing through the lower river. We used the daily estimates to determine the run timing patterns of the individual stocks and regional components of the return.

The number of radio-tagged fish released on day t was denoted as $R = (R_1, \ldots, R_t)'$. These fish were assumed to represent a random sample from the mixture of Chinook Salmon stocks passing through the tagging area each day. A total of 46 final destinations (designated as stocks) were included in the analysis, and the unknown stock proportions of the mixture on day t were denoted by $\theta_t = (\theta_{t,1}, \ldots, \theta_{t,46})'$. Final destinations included 42 terminal areas with confirmed spawning activity and four nonterminal areas. The numbers of fish escaping to spawning areas from releases on day t were denoted as $r_t = (r_{t,1}, \ldots, r_{t,46})'$.

Fifteen fisheries upriver from the tagging area were defined for the analysis (Figure 2); 14 of these (fisheries 1 through 14) may have altered the stock composition estimates at the tagging site because they disproportionally intercepted stocks traveling to upriver spawning areas (i.e., stocks traveling farther upriver were exposed to more fishing pressure than those in the lower river). The first fishery (fishery 0) was downstream of all upriver spawning areas, and therefore all of these stocks were vulnerable to being harvested. Radio-tagged

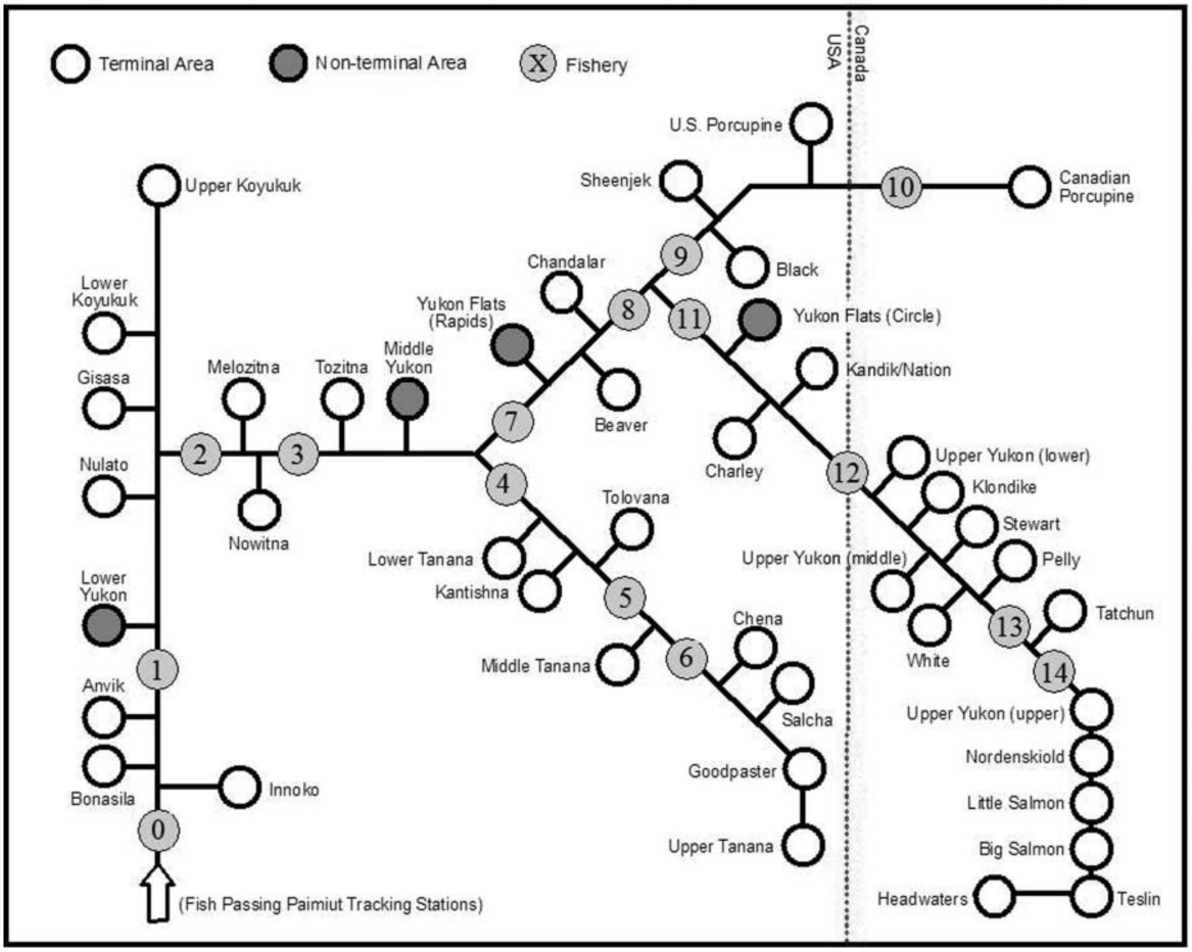

FIGURE 2. Migration model for calculating stock composition estimates of Chinook Salmon returns in the Yukon River basin based on the distribution of radio-tagged fish, weighted by daily measures of abundance at the tagging site, and adjusted to account for tagged fish removed in upriver fisheries. The spatial relationships of the fisheries and component stocks are indicated; the numbers denote the fisheries in the model.

fish caught in fishery 0 were subtracted from the initial releases to provide a corrected set of daily releases, namely, $R = (R_1, \ldots, R_t)'$, and were not considered further in this analysis. Fish destined for any spawning stock s were exposed to a downriver subset of the 14 remaining fisheries. The collection of these fishery indices is denoted by F_s. Catches in the 14 fisheries from releases of day t are denoted by $C_t = (c_{t,1}, \ldots, c_{t,14})'$, and the corresponding exploitation rates (i.e., the fractions of the tagged fish entering and being removed by each fishery) were denoted by $\phi_t = (\phi_{t,1}, \ldots, \phi_{t,14})'$. The set of stock indices of upriver stocks passing through fishery f are denoted by S_f, where $f = 1, \ldots, 14$.

Observed counts of radio-tagged fish among spawning areas and catches were modeled so that the effects of unequal harvests among the stocks would not bias the estimates of stock composition at the tagging site. A probability model was developed using the schematic for the migration routes, fisheries, and spawning areas in the Yukon River basin (Figure 2). Counts of fish in the escapements and catches from a daily release were assumed to have the multinomial distribution,

$$p(r_{t,1}, \ldots, r_{t,46}, c_{t,1}, \ldots, c_{t,14}) = \left(\frac{R_t!}{\prod_{s=1}^{46} r_{t,s}! \prod_{f=1}^{14} c_{t,f}!} \right) \prod_{s=1}^{46} (\theta_{t,s}\psi_{t,s})^{r_{t,s}} \times \prod_{f=1}^{14} (\mu_{t,f})^{c_{t,f}}$$

and

$$\sum_{s=1}^{46} \theta_{t,s}\psi_{t,s} + \sum_{f=1}^{14} \mu_{t,f} = 1, \quad t = 1, \ldots, T, \tag{1}$$

where $\psi_{t,s} = \prod_{j \in F_s} (1 - \phi_{t,j})$ is the probability that a fish destined for stock s escapes downriver fisheries, $\mu_{t,f} = \prod_{j \in H_f} (1 - \phi_{t,j}) \phi_{t,f} \sum_{s \in S_f} \theta_{t,s}$ is the probability that a tagged fish released on day t is caught in fishery f, and H_f is the set of indices for fisheries downstream from fishery f. The Lagrange function for the unknown parameters given the recoveries and catches from day t, which is the likelihood function with an added term to constrain the daily probabilities to equal 1, is

$$\log L(r,c;\theta_t,\phi_t) = \kappa + \sum_{s=1}^{46} r_{t,s}\log(\theta_{t,s}\psi_{t,s}) + \sum_{f=1}^{14} c_{t,f}\log(\mu_{t,f}) + \gamma\left(\sum_{s=1}^{46}\theta_{t,s}\psi_{t,s} + \sum_{f=1}^{14}\mu_{t,f} - 1\right), \quad (2)$$

where κ is a constant and γ is a constant called the Lagrange multiplier. The Lagrange function was maximized by values of $\theta_{t,s}$, as shown in Table 4 of Eiler et al. (2006) with known values of $\phi_{t,f}$ given by

$$\phi_{t,f} = c_{t,f}\Bigg/\left(R_t - \sum_{s\in G_f} r_{t,s} - \sum_{j\in H_f} c_{t,j}\right), \quad f = 1,\ldots,14, \quad (3)$$

where G_f is the set of indices for stocks downstream from fishery f. Although the estimates of daily stock composition were of interest, they do not reflect the changes in magnitude of the daily returns passing Russian Mission. The unknown daily numbers of fish passing this site were denoted as $E_1, E_2, \ldots, E_T$, and their season total as $E_. = \sum_{i=1}^{T} E_i$. The daily fractions of the total return passing the tagging area were denoted as

$$\pi_i = E_i/E_., \quad i = 1,\ldots,T. \quad (4)$$

The daily fractions of the total season return to the basin that pass the capture site were estimated from the catch rates of the gill nets used to capture the fish for tagging. Gill nets were expected to capture fish in proportion to daily effort. Daily catches, $X_1,\ldots,X_T$, were assumed to be Poisson random variables with expected values,

$$\lambda_t = \lambda h_t E_t = (\lambda E_.)h_t\frac{E_t}{E_.} = \lambda_0 h_t \pi_t, \quad t = 1,\ldots,T, \quad (5)$$

where $\lambda_0 = \lambda E_.$ is a constant proportional to the total return and h_t is the number of units of effort on day t. Maximum likelihood estimates of the daily migration fractions, $\pi = (\pi_1,\ldots,\pi_T)'$, can be shown to be the time series of normalized catch per effort,

$$\hat{\pi}_t = Y_t\Bigg/\sum_{j=1}^{T} Y_j = (X_t/h_t)\Bigg/\left(\sum_{t'=1}^{T} X_{t'}/h_{t'}\right), \quad t = 1,\ldots,T. \quad (6)$$

The maximum likelihood estimate of λ_0 is $\hat{\lambda}_0 = \sum_{t=1}^{T} X_t/h_t$.

The daily fractions of the total season return to the basin that are destined for any particular stock equal the products of the stock's daily proportions, $\theta_{t,s}$, and the corresponding daily fractions of the total season return passing the tagging site, namely, $\omega_{t,s} = \pi_t\theta_{t,s}$. These stock-specific daily fractions of the total return were estimated by the daily products of the estimates of stock composition, $\theta_{t,s}$, and the daily migration fractions, $\hat{\pi}_t$, from equation (6),

$$\hat{\omega}_{t,s} = \hat{\pi}_t\hat{\theta}_{t,s}, \quad s = 1,\ldots,46; t = 1,\ldots,T. \quad (7)$$

Finally, the estimated fraction of the total season return to the Yukon River basin that belonged to any stock s equals the sum,

$$\hat{\alpha}_s = \sum_{t=1}^{T}\hat{\omega}_{t,s}, \quad s = 1,\ldots,46. \quad (8)$$

To evaluate the sampling variation in estimates, a parametric bootstrap was performed. First, random bootstrap samples of daily gill-net catches, $X_1^*, X_2^*, \ldots, X_T^*$, were drawn from Poisson distributions with expected values of the X_t^* determined from the maximum likelihood estimates and equal to $\hat{X}_t = \hat{\lambda}_0 h_t\hat{\pi}_t$, $t = 1, 2, \ldots, T$. These random catches were used to compute the corresponding bootstrap catch rates, $Y_1^*, Y_2^*, \ldots, Y_T^*$, and the daily migration fractions, π_t^*, $t = 1, \ldots, T$. Next, independent daily multinomial samples of radio-tagged fish, either migrating to the possible stocks, $r_{t,1}^*, r_{t,2}^*, \ldots, r_{t,46}^*$, or caught in the various fisheries, $c_{t,1}^*, c_{t,2}^*, \ldots, c_{t,14}^*$, from the daily known numbers released, R_t, were drawn with probabilities equal to the original maximum likelihood estimates from equation (1).

Bootstrap samples of tagged fish in catches and escapements were used to compute the corresponding bootstrap estimates for stock proportions, such as $\hat{\theta}_{t,s}$, just as with the original counts of tagged fish. Finally, bootstrap estimates for the stock proportions were weighted by the bootstrap daily migration fractions. The next bootstrap sampling began with another draw of the daily gill-net catches and the tagged numbers migrating to the possible stocks or caught in the fisheries, followed by computation of the bootstrap estimates of daily catch rates, daily migration fractions, daily stock compositions, and weighted stock compositions.

Stock composition estimates were based on the assumption that fish allocated to designated stock groups (both terminal and nonterminal) represented spawning populations. However, nonterminal reaches that included fish in transit to spawning areas farther upriver (i.e., undocumented fishery harvests and fish that died due to disease, injury, poor physical condition, or predation prior to reaching their final destination) would bias the composition estimates and underestimate the contribution of upriver stocks. To address this concern, stock composition estimates were recalculated for comparison, with all fish remaining in nonterminal areas being categorized as in-transit and treated as fishery recoveries in the model.

Inter-annual differences in stock-group composition estimates were tested using a multivariate test for proportions described by Edgington (1995). Stock composition estimates for each year were computed as sums over the season point estimate (equation 8) for the individual stocks of the regional groups. Edgington's test statistic, which is based on a geometrical approach, is the sum of squared deviations from proportion means summed over the dependent variables and weighted by sample size. Following Edgington's notation (1995), we defined the test statistic with no weighting as

$$SS = SS_1 + SS_2 + \ldots + SS_W,$$

where

W = the number of stock groups,

$SS_i = (B_{i,2002} - \overline{B}_i)^2 + (B_{i,2003} - \overline{B}_i)^2 + (B_{i,2004} - \overline{B}_i)^2,$

$B_{i,\text{year}}$ = the composition estimate for stock group i of that year, and

$\overline{B}_i$ = the composition estimate for stock group i averaged over the 3 years.

The significance of the test was determined from the reference distribution generated from the parametric bootstrap that was used in evaluating the sampling variation in the stock composition estimates. The test statistic was computed for each of the bootstrap composition estimates, and the P-value was determined as the proportion of test statistics that were greater than or equal to the observed test statistic.

RESULTS

Capture and Tagging

We started fishing in early June and continued until the end of the run in mid-July, when catch rates were low (Table 1). Tagging operations were delayed until 9 June in 2002, and it is likely that the earliest fish passing through the lower river were not sampled. However, harvest data from fisheries near the river mouth (JTC 2002) suggest that any loss in coverage due to the delay was minimal. The drift gill nets designed for the study were effective at capturing Chinook Salmon in a condition suitable for tagging based on the number of uninjured and physically active fish caught. Bycatch was minimal, even though large numbers of summer Chum Salmon were moving through the lower river during this period.

Annual differences in run timing were observed based on catch per unit effort (CPUE) data from the Russian Mission tagging site (Figure 3). In 2002, several distinct pulses of fish moved through the lower river from early to mid-June, with declining numbers during late June and July. The 2003 return exhibited a more bell-shaped curve. Although several pulses of fish were observed in early and late June, the peak of the run was pronounced, with most fish passing Russian Mission during 15–19 June. The peak of the run was less pronounced in 2004, with several distinct pulses moving through the lower river during middle and late June.

A total of 2,860 Chinook Salmon were radio-tagged during the 3 years of the study, with transmitters deployed throughout the run (Figure 3). Six-year-old fish were the dominant age-class (67.2%), ranging from 63.2% to 69.3% of the sample. The remaining fish were primarily 5-year-olds (20.5%, ranging from 18.1% to 22.1%), with smaller proportions of 7-year-old (8.1%), 4-year-old (4.1%), 8-year-old (0.07%), and 3-year-old fish (0.03%). Most of these fish (99.8%) resided in freshwater for 1 year prior to migrating to sea, with only five fish remaining for a second year. Fish length averaged 833 mm (ranging from 395 to 1,075 mm) and was similar across years based on box plots of the data. Fish passing through the lower river were primarily bright, iridescent silver in color during the first several weeks of June, with increasing numbers of dull silver fish later in the run. Small numbers of blush-colored fish were observed from mid-June to the end of the run. This general pattern was observed across years, although the prevalence of iridescent silver fish was nominally greater over the course of the run in 2003. Color differences were also observed in

TABLE 1. Tagging dates and numbers of Chinook Salmon captured, tagged, tracked upriver, and not located upriver after release for fish radio-tagged in the lower Yukon River during 2002–2004. Percentages of the total fish tagged are in parentheses.

Date or category	2002	2003	2004	All years
Start of tagging	9 Jun	3 Jun	3 Jun	3–9 Jun
End of tagging	13 Jul	14 Jul	19 Jul	13–19 Jul
Captured	1,310	2,312	2,107	5,729
Tagged	768	1,097	995	2,860
Moved upriver	751 (97.8)	1,081 (98.5)	958 (96.3)	2,790 (97.6)
Upriver location[a]	481 (62.6)	810 (73.8)	625 (62.8)	1,916 (67.0)
Harvested in fishery	270 (35.2)	271 (24.7)	333 (33.4)	874 (30.6)
Not located upriver	17 (2.2)	16 (1.5)	37 (3.7)	70 (2.4)

[a]Fish located upriver from Paimiut tracking stations.

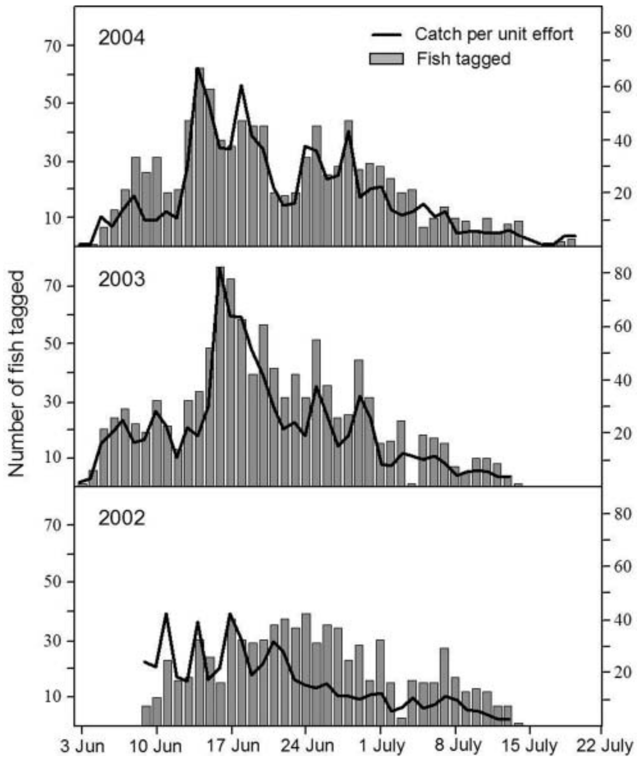

FIGURE 3. Daily catch per unit effort based on the number of fish caught by minutes fished for Chinook Salmon captured at the Russian Mission tagging site, and the number of Chinook Salmon radio-tagged during 2002–2004.

relation to the final destination of the fish. Most fish traveling to the upper basin were iridescent silver when captured in the lower river (e.g., 83.6% and 86.8% for Upper Porcupine (the upper portion of the Porcupine River and its associated tributaries) and Upper Yukon fish, respectively), while fish destined for spawning areas lower in the basin were increasingly dull silver in color, ranging from 40.8% to 46.7% for fish returning to the Koyukuk, Tanana, and Yukon flats and from 63.9% to 82.9% for those returning to the Middle Yukon and Lower Yukon. Blush-colored fish were primarily late-run fish returning to lower basin tributaries (e.g., 8.8% and 9.8% for Lower Yukon and Middle Yukon stocks, respectively).

Tagging Response

Most fish (2,790 [97.6%]) resumed upriver movements after release (Table 1) and were either harvested in fisheries (874 [30.6%]) or traveled to upriver reaches of the basin (1,916 [67.0%]). Similar results were observed across years. Seventy fish (2.4%) were not located upriver and either regurgitated their transmitters; died after release due to handling, predation, or undocumented encounters with local fishers; or had transmitters that malfunctioned. None of the fish harvested in upriver fisheries, examined at assessment projects, or recovered on the spawning grounds were missing their transmitters (i.e., both the transmitters and external spaghetti tags were present), suggesting that regurgitation was not a major factor. Similarly, all of the transmitters recovered were functioning, which, combined with the high tracking success at the stations, suggests that the vast majority of fish that moved upriver were identified.

Most fish passed Paimiut several days after release, averaging 1.6 and 3.4 d for fish tagged near Russian Mission and Marshall, respectively. However, the migration rates observed after tagging suggest that the fish were initially affected by the capture, handling, and tagging methods (hereafter referred to collectively as the tagging effect). Fish exhibited progressively faster swimming speeds as they moved farther away from the tagging site (Figure 4). Migration rates at Paimiut for fish tagged near Russian Mission (29–94 km downriver) averaged 34.4 km/d (95% confidence interval, 33.7–35.1 km/d), compared with 44.7 km/d (42.5–46.9 km/d) for fish tagged near Marshall (139–154 km downriver). There was convincing evidence of a positive relationship between migration rate and the distance fish traveled to reach Paimiut ($P < 0.001$, df = 1,256), with fish moving 1.4 km/d faster on average for every 10 km increase in distance traveled after release.

A similar pattern was observed as these fish continued moving upriver. Most fish (1,234 [98%]) displayed an increase in swimming speed between Paimiut and the Yukon–Anvik River confluence (Figure 4), with migration rates for individual fish increasing on average by 22.0 km/d. Differences in migration rates between these two sites were less for fish tagged at Marshall, with swimming speeds increasing on average by 15.6 km/d (95% confidence interval, 13.7–17.5 km/d), compared with 22.6 km/d for Russian Mission fish

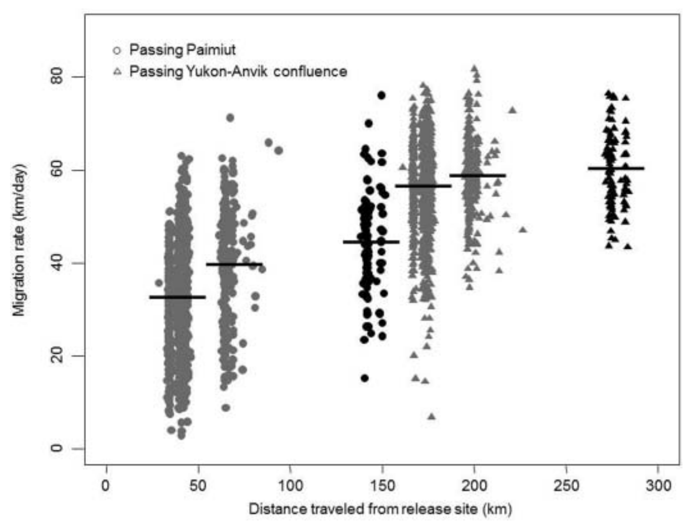

FIGURE 4. Migration rates of radio-tagged Chinook Salmon passing remote tracking stations in the lower Yukon River near Paimiut and the Yukon–Anvik River confluence. The fish were captured with drift nets (varying release sites) near the villages of Russian Mission (gray symbols) and Marshall (black symbols). Average migration rates by distance traveled from the release site are also indicated (horizontal bars).

(22.0–23.2 km/d). These findings suggest that Marshall fish had recovered more by the time they reached Paimiut and as a result were showing less difference in swimming speeds than fish released closer to Paimiut. The geomorphic and hydrological characteristics of these two consecutive reaches were similar, suggesting that the differences observed primarily reflected the time since release and distance traveled rather than the conditions encountered by the fish.

Fishery Recoveries

Radio-tagged fish were harvested throughout the basin, representing between 25% and 35% of the tagged sample annually (Table 1). Most of these fish (659 [75.4%]) were harvested in U.S. fisheries along the main stem, with smaller numbers being caught in the Tanana (69 [7.9%]), Koyukuk (8 [0.9%]), and Porcupine (1 [0.1%]) rivers. Fish harvested in main-stem fisheries were likely composed of both U.S. and Canadian stocks, although fish caught near Eagle, Alaska (just downstream from the U.S.–Canada border) were assumed to be destined for spawning areas in Canada. Canadian catches were primarily harvested in main-stem reaches (82 [9.4%]) and several large tributaries (48 [5.5%]). Small numbers of fish were also caught in Canadian reaches of the Porcupine River (7 [0.8%]).

Based on aerial surveys that included villages along the main stem and Tanana River, over 200 (27%) of the 737 radio-tagged fish harvested by U.S. fishers were not reported, comprising 20.9, 29.7, and 30.4% annually. A similar phenomenon was observed in Canadian reaches, although the extent was more difficult to assess due to the proximity of some Canadian fisheries to possible spawning areas.

Upriver Distribution

Radio-tagged fish traveled to areas throughout the basin with 2,120 fish recovered in terminal fisheries or tracked to localized areas (Figure 5). Most of the fish returned to the Tanana (n = 502) and Upper Yukon (n = 953). Substantially fewer fish were tracked to terminal areas in the other regions, ranging from 44 fish in the Upper Koyukuk to 147 fish in Lower Yukon tributaries. The distribution within regions typically consisted of fish clustered in one or two principal tributaries, with smaller numbers spawning in other isolated areas. For example, 105 (71.2%) of the 147 fish returning to Lower Yukon tributaries were tracked to spawning areas in the Anvik River. Fish returning to the Upper Yukon were more widely dispersed, although the overall distribution was still relatively clumped (Figure 5). In addition to the fish tracked to terminal tributaries, 201 fish were last located in nonterminal reaches of the U.S. main stem. Although nominal differences were observed annually, both the regional and stock-specific distribution patterns were similar across years (Tables A.1 and A.2 in the appendix to this article).

Differences were observed in the spawning distributions of fish within their terminal tributaries. Upper Yukon fish returning to the Teslin River displayed a negative relationship between run timing and the distance traveled after reaching the tributary mouth. Fish tagged early in the run traveled primarily to spawning areas in the upper reaches, whereas later-run fish generally spawned in lower reaches of the drainage. However, this observation was not typical of the return. Fish returning to most terminal tributaries either exhibited no relationship or a slightly negative relationship between distance traveled and run timing. Of the four principal stocks returning to the Upper Yukon, comparable numbers of early- and late-run fish traveled to the upper reaches of the Stewart, Pelly, and Big Salmon rivers (Figure 6). A similar pattern was observed for the other major and minor stocks within the basin.

Spawning Areas

Most fish returned to clear water tributaries that were relatively entrenched, had moderate gradients, and were associated with relatively narrow valleys and gentle slopes. These areas were collectively classified as rolling uplands (similar to categories described by Brabets et al. 2000). Fish were largely absent in lowland reaches characterized by meandering, low gradient, highly alluvial channels associated with main river floodplains, and in the moderately rugged reaches associated with nearby mountainous slopes.

Although the river types used were generally similar across regions, some differences were observed. Most of the fish in the Lower Yukon, Middle Yukon, Upper Koyukuk, and Upper Porcupine traveled to upland areas located on the periphery of the main river floodplain. A similar pattern was observed in the Yukon Flats except for fish returning to the Sheenjek River, which also spawned in lowland reaches of the drainage (Figure 7). Although distant from the main stem (~70 km), Chandalar River fish spawning lower in the drainage also utilized lowland areas. Most Tanana fish returned to upland tributaries, in particular the Chena, Salcha, and Goodpaster rivers. Fish were distributed widely within these rivers, spawning from sites near the river mouth to the upper reaches (Figure 7). Tolovana River fish were conspicuously absent in reaches near the river mouth (classified as lowlands), traveling instead to upland areas in the upper portion of the drainage. Relatively few fish returned to the numerous tributaries flowing north across the Tanana Flats, although small clusters were located in the Kantishna and Nenana rivers and individual fish were periodically tracked to small tributaries associated with the main river.

The Upper Yukon consists primarily of upland areas with moderately rugged mountainous slopes along the periphery. Most Upper Yukon fish returned to upland areas and were largely absent from the more mountainous reaches. A notable exception was the Big Salmon River, which was

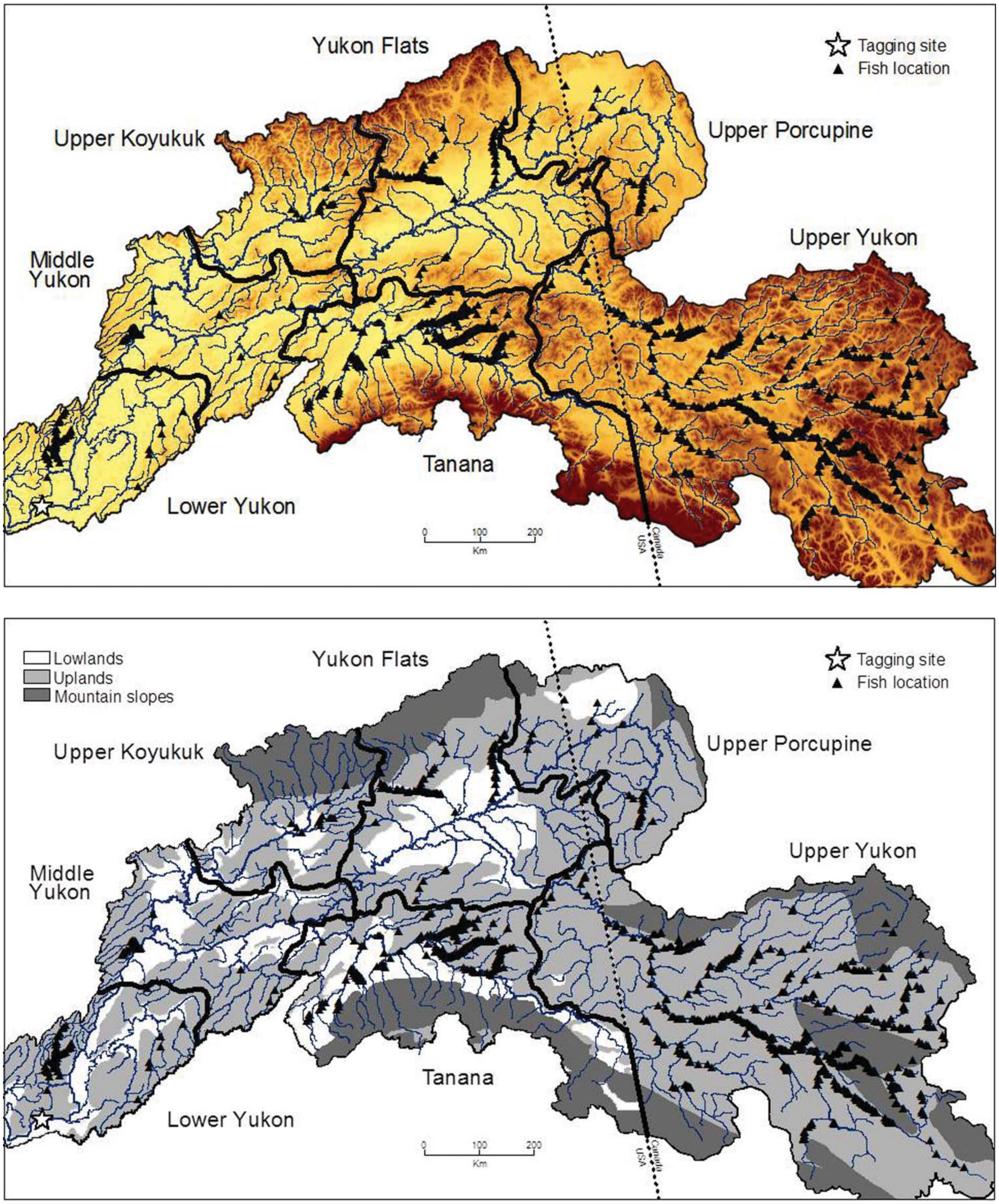

FIGURE 5. Final locations of Chinook Salmon radio-tagged in the lower Yukon River during 2002–2004. Regional areas, the location of the tagging site, basin topography (upper panel), and physiographic features (lower panel) are indicated. Topographic and physiographic overlays were provided by the U.S. Geological Survey. [Color figure available online.]

classified as mountainous and had sizable numbers of fish returning during all 3 years of the study. Small numbers of fish also returned to mountainous reaches associated with the upper headwaters of the Koyukuk and Chandalar rivers.

Stock Composition

Chinook Salmon returns consisted primarily of Tanana and Upper Yukon fish, collectively comprising between 71.5% and 72.5% of the return during the 3-year study. Upper Yukon

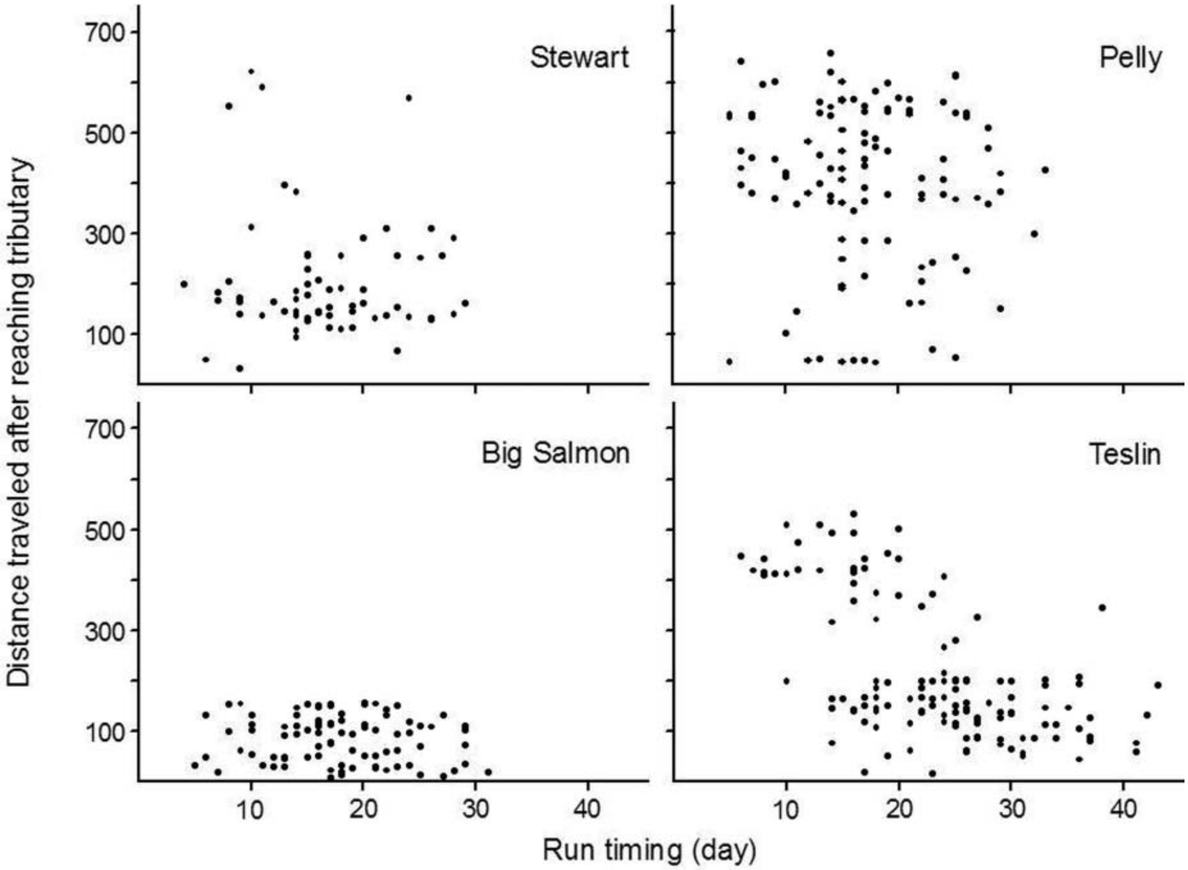

FIGURE 6. Comparison of the distances traveled by Chinook Salmon after arriving at their terminal tributaries in relation to run timing based on capture date at Russian Mission. Fish representing four principal stocks returning to the Upper Yukon are shown, including three stocks returning to large-tributary drainages (Stewart, Pelly, and Teslin) and one stock returning to a smaller tributary (Big Salmon) with fish traveling <200 km from the tributary mouth to reach spawning sites. June 5 was designated as day 0 for run timing.

fish were the largest component, ranging from 47.2% to 52.3% of the return (Figure 8). Most of these fish (28.0–32.7% of the return) traveled to several large (Stewart, Pelly, and Teslin rivers) and medium-sized (Big Salmon River) tributaries (Figure 9). A number of minor stocks were also present, with average composition estimates ranging from 0.3% (Charley River) to 2.6% (White River). Collectively, these minor stocks represented between 8.1% and 10.0% of the return. Upper Yukon fish also remained in main-stem areas, principally in the middle (upstream of the Yukon–Stewart River confluence) and upper (upstream of the Yukon–Pelly River confluence) reaches, comprising 3.8–4.8% and 4.4–5.3% of the return, respectively.

Tanana fish were also a major regional component, ranging from 19.3% to 24.3% of the return (Figure 8). This assemblage also consisted of a combination of major and minor stocks (Figure 9), with most fish (15.6–18.8% of the return) traveling to the Chena, Salcha, and Goodpaster rivers. Unlike the Upper Yukon fish, minor stocks represent a substantially smaller proportion of the return (1.5–1.7%). Tanana fish also remained in the main river and small associated tributaries, primarily in the middle and upper reaches of the drainage.

By comparison, the components of the run returning to the Yukon Flats and the Upper Porcupine were relatively small (Figure 8). Upper Porcupine stocks ranged from 2.1% to 3.9% of the return, with most fish traveling to upper headwaters. Composition estimates for fish returning to tributaries within the Yukon Flats ranged from 3.3% to 6.9% of the return, with Chandalar River fish (1.7–4.0%) and Sheenjek River fish (1.0–2.5%) comprising the principal stocks (Figure 9). Substantially smaller percentages of the run returned to the Black River and Beaver Creek. Fish also remained in nonterminal reaches of the main stem, ranging from 3.7% to 4.6% of the return.

Chinook Salmon also returned to spawning areas in the lower and middle basin. Composition estimates for Lower Yukon tributaries ranged from 3.3% to 6.1% of the return (Figure 8). This component was composed primarily of Anvik River fish (2.6–4.1%), with smaller proportions returning to the Innoko and Bonasila rivers (Figure 9). Middle Yukon stocks, consisting of fish traveling to medium-sized tributaries

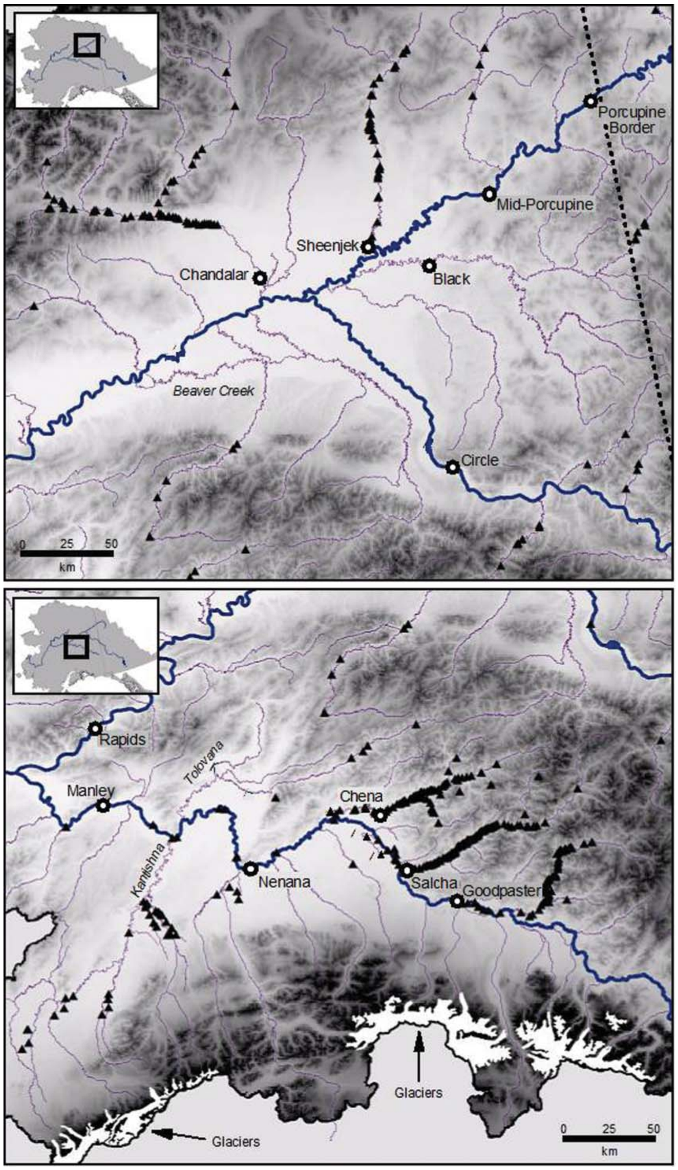

FIGURE 7. Distributions (triangles) of Chinook Salmon radio-tagged in the lower Yukon River and tracked to terminal spawning areas in the Yukon Flats (upper panel) and Tanana River (lower panel) during 2002–2004. Topographic overlays were provided by the U.S. Geological Survey. [Color figure available online.]

along the Yukon River corridor and lower Koyukuk River, were also relatively minor components, with most fish returning to the Nulato (1.3–1.9%) and Tozitna (1.0–1.2%) rivers and smaller proportions to the Gisasa, Melozitna, and Nowitna rivers. Similarly, headwater stocks in the Upper Koyukuk were a minor component, ranging from 1.1% to 1.9% of the return. As in the upper basin, fish remained in nonterminal reaches of the main stem, ranging from 2.9% to 5.7% of the return in the Lower Yukon and from 0.8% to 1.5% of the return in the Middle Yukon.

Stock composition estimates were relatively consistent across years (Table A.3). There was no evidence of interannual differences by region (sum of squares = 0.0048, P = 0.80), suggesting that the relative contribution of the regional components was fairly stable during this period. A similar pattern was observed for individual stocks. Only the Little Salmon River showed substantial differences across years, with a higher proportion of the run returning to this tributary in 2003 (Figure 9). Ancillary observations on the spawning grounds also reflected this pattern. The composition estimate for Salcha River fish was noticeably lower in 2003, but within the bounds of the 95% confidence intervals of the other years.

Composition estimates derived using the two treatments of nonterminal fish (i.e., all fish treated as local spawners versus all fish treated as in transit to spawning areas farther upriver) were similar (Figure 10). Upper Yukon fish were most discordant, with estimates of 50.6, 51.6, and 46.7% of the return (2002–2004, respectively) when nonterminal fish were considered to be local spawning populations, compared with 56.7, 57.9, and 53.8% of the return when these fish were treated as in transit to spawning areas farther upriver. Stock composition estimates for Tanana fish increased to a lesser extent: from 20.9, 19.3, and 24.4% when nonterminal fish were treated as spawning populations to 21.6, 20.4, and 26.2% when nonterminal fish were assumed to be in transit to upriver areas. Differences in stock composition estimates for the other regions were minimal (i.e., less the 1%).

Stock Timing

Chinook Salmon passing through the lower Yukon River (i.e., moving past Russian Mission) exhibited different run timing patterns. Tanana and Upper Yukon fish were present throughout the run but were most abundant from middle to late June (Figure 11). Although substantially less abundant, fish traveling to the Yukon Flats and the Middle Yukon exhibited a similar pattern. Lower Yukon fish displayed later run timing, with most passing Russian Mission during late June and July. These regional patterns were consistent during the 3 years of the study, with median run timing prior to 20 June for Upper Yukon, Yukon Flats, and Tanana fish, compared with early July for Lower Yukon fish (Figure 11). Run timing for Middle Yukon fish was consistently earlier than for the Lower Yukon component but generally later than for fish traveling farther upriver, particularly during 2002.

Run timing differences were also observed among individual stocks. The time taken to move past Russian Mission averaged 28 d, ranging from 16 (Klondike River fish) to 38 d (Teslin River fish), with several stocks being present throughout the run (Figure 12). In the Upper Yukon, the timing of Klondike and Stewart River fish was early (median passage prior to 17 June) and relatively discrete, whereas fish traveling to tributaries farther upriver (e.g., Teslin River fish) exhibited later and more protracted run timing. The three dominant

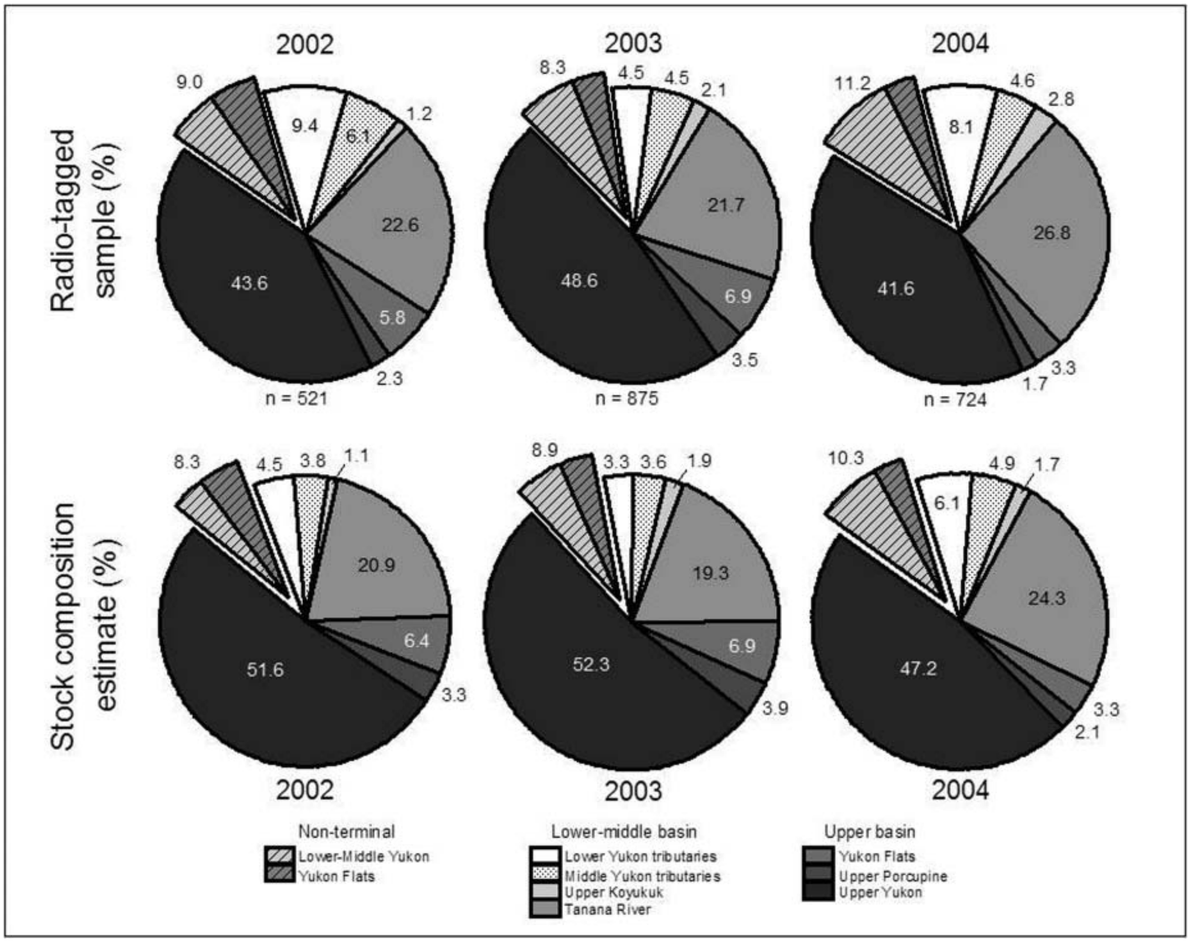

FIGURE 8. Comparison of the regional distributions of Chinook Salmon radio-tagged in the lower Yukon River during 2002–2004, and stock composition estimates based on the distribution data weighted by daily measures of abundance at the tagging site and adjusted to account for the harvest of tagged fish in upriver fisheries.

Tanana stocks (Chena, Salcha, and Goodpaster rivers) exhibited similar timing patterns, with most fish passing Russian Mission from middle to late June, but with fish present from early June to middle July. In contrast, Tanana fish returning to the Kantishna River had later and more compressed run timing.

Run timing was generally later for stocks traveling shorter distances upriver. The stocks returning to the spawning tributaries closest to Russian Mission (e.g., the Bonasila and Anvik rivers, which are located approximately 160 and 180 km upriver, respectively) exhibited the latest timing, with median passage in early July (Figure 12). By comparison, 50% of the Klondike River fish (which traveled in excess of 1,800 km to reach their terminal tributary) passed Russian Mission prior to mid-June. However, run timing was comparable for most middle and upper basin stocks, particularly during 2003 and 2004, even though the distances traveled ranged from 700 to 2,300 km. The principal exceptions were fish traveling to headwater areas in the Upper Yukon (distances in excess of 2,400 km from Russian Mission), which displayed later run timing than other upper-basin stocks (Figure 12). It should also be noted that the distances used in these comparisons were minimum estimates, reflecting the distance fish traveled from Russian Mission to the mouth of their terminal tributary. Many fish returning to large Upper Yukon tributaries (the Stewart, White, Pelly, and Teslin rivers) traveled substantially farther upriver after reaching their terminal tributary than fish returning to the small and medium-sized spawning tributaries typical in other regional areas, suggesting an even weaker relationship between stock timing and distance traveled.

The timing patterns of individual stocks were relatively consistent during the 3 years of the study. Annual differences in lower-river passage were typically less than 5 d for most stocks, using the 50th percentile as a relative measure of run timing (Figure 12). Small sample sizes for some stocks, such as the Gisasa and Tozitna River fish in 2002, resulted in imprecise timing estimates.

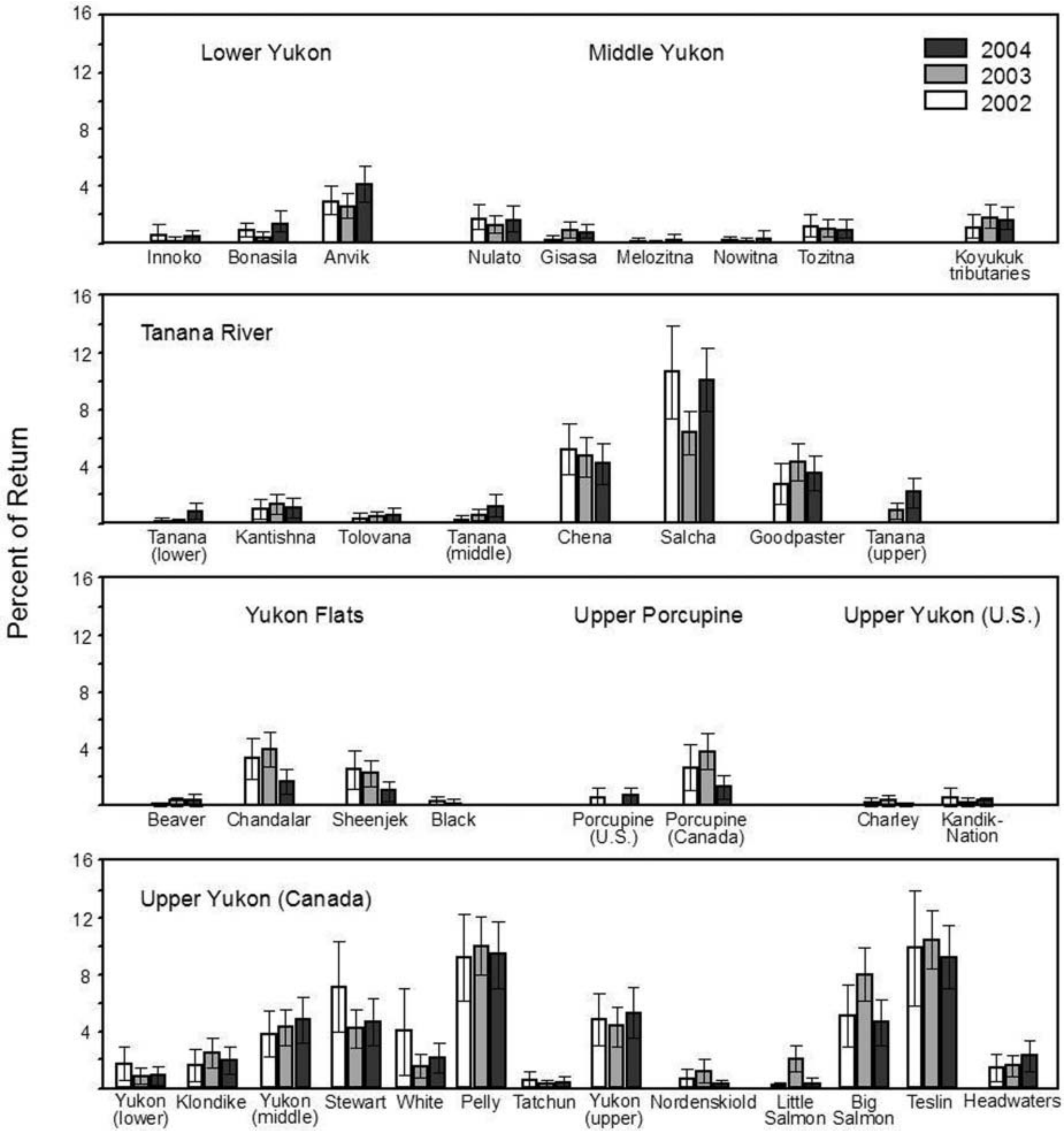

FIGURE 9. Stock composition of Chinook Salmon stocks returning to terminal reaches of the Yukon River basin in 2002–2004, based on the distribution of radio-tagged fish weighted by catch per unit effort information at the Russian Mission tagging site and adjusted for the harvest of tagged individuals in upriver fisheries. Error bars = 95% confidence intervals.

DISCUSSION

Information on the spawning distribution, stock composition, and run timing, used in conjunction with estimates of run abundance, is essential for understanding and managing salmon returns in large river basins. This is particularly true in drainages with widely scattered fisheries and varying harvest regimes, which can have differential impacts on individual stocks and over time affect the overall stock structure of the return. In spite of the logistical challenges encountered during the study, the methods used to tag and track Yukon River Chinook Salmon were remarkably successful and provided detailed information on upriver dispersal, final destinations, stock structure, and stock-specific run timing.

Spawning Distribution

Chinook Salmon returns consisted of an aggregate of spatially distinct populations, with fish returning to spawning

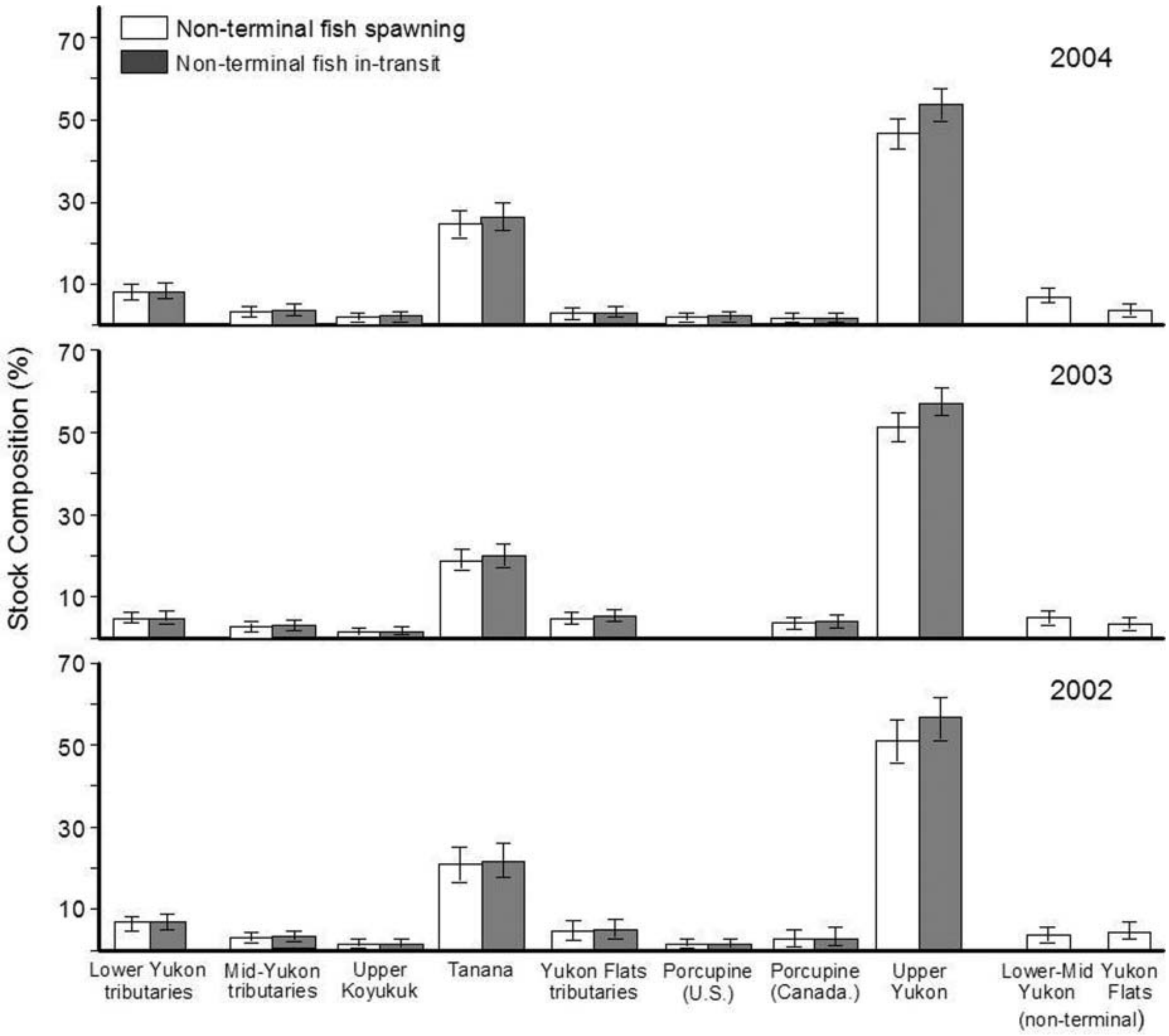

FIGURE 10. Comparison of regional stock composition estimates of Yukon River Chinook Salmon returns in 2002–2004 based on the presumed status of fish remaining in nonterminal reaches of the U.S. Yukon River main stem (i.e., categorized as fish in transit to spawning areas farther upriver or fish spawning in local areas). Nonterminal areas include associated main-stem tributaries not monitored during the study. Error bars = 95% confidence intervals.

areas throughout the basin. Fish in the Upper Yukon were widely distributed, whereas those returning to the other regions were conspicuously clumped in isolated areas. Similar distribution patterns were observed across years, suggesting that the principal components of the run were identified with both major and minor stocks being represented. There was good agreement between the final destination of the fish tracked to upriver areas and GSI composition estimates derived from the tissue samples taken from the tagged sample (Flannery et al. 2012), indicating that the fish were returning with relative precision to natal streams.

Information is not available on how larger escapements might impact the distribution of Chinook Salmon within the basin; escapement estimates during our study ranged from poor to average compared with those prior to the 1998 decline in run abundance (JTC 2002, 2004, 2005). The distribution of both radio-tagged and untagged Chinook Salmon returning to the Taku River, a large coastal drainage in Alaska and northwestern British Columbia, extended beyond the designated index areas used to assess run abundance (J. H. Eiler, unpublished report). These index areas were initially established when escapement levels were low (P. Kissner, Alaska Department of Fish and Game, personal communication), suggesting that the original distribution reflected optimal spawning habitat and that the areas used by spawning salmon expanded as escapement increased.

Site selection by spawning salmon has been attributed to a variety of factors, including thermal and flow regimes, channel morphology, substrate characteristics, and accessibility (Neilson and Banford 1983; Lorenz and Eiler 1989; Berman and Quinn 1991; Geist and Dauble 1998; Isaak et al. 2007). Yukon River Chinook Salmon presumably have similar strategies,

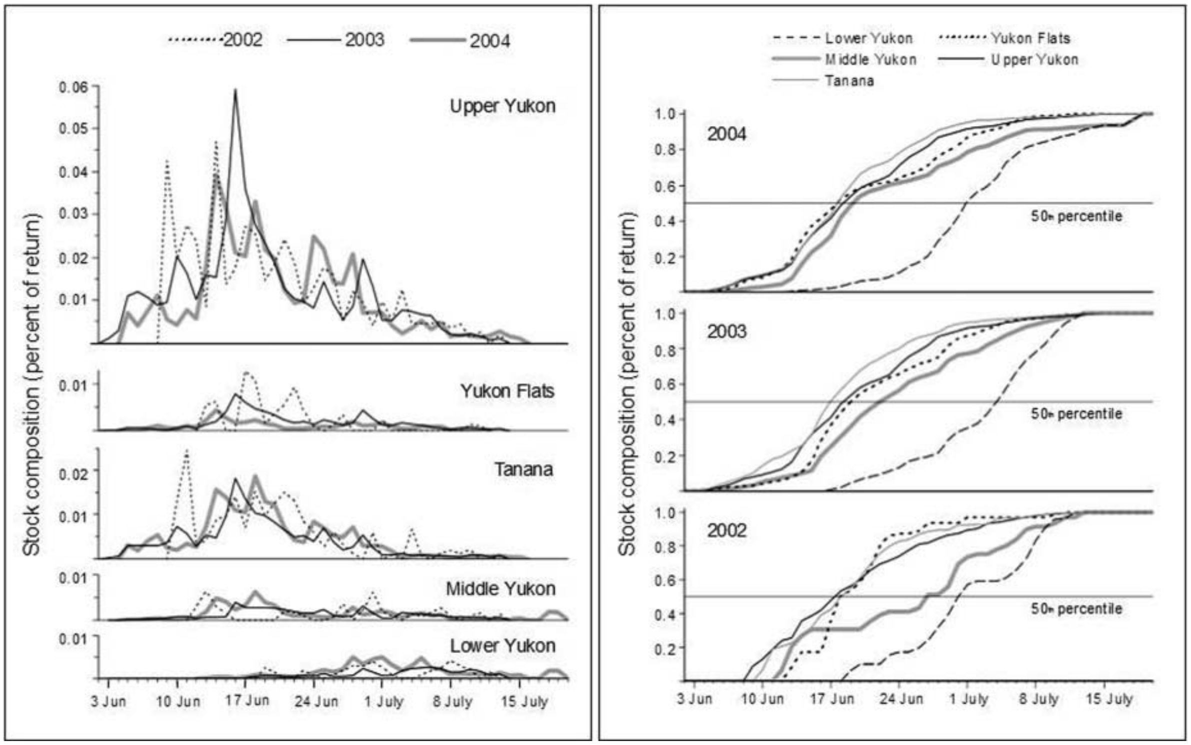

FIGURE 11. Lower-river run timing of regional aggregates of Chinook Salmon returning to terminal reaches of the Yukon River basin in 2002–2004 based on daily stock composition estimates. The daily percentages of the return (left panel) and cumulative percentages of the regional returns (right panel) are shown by regional components. The 50th percentile is indicated for the cumulative percentages.

selecting sites that facilitate spawning activities; enhance egg deposition, development, and survival; and provide access to suitable juvenile rearing areas. However, detailed information on habitat characteristics within the basin is limited and typically restricted to localized areas (Durst 2001; unpublished report on the utilization of habitats by Chinook, Chum, and Coho Salmon in the Yukon River basin in Canada by A. von Finster, Department of Fisheries and Oceans Canada, Habitat and Enhancement Branch, Whitehorse, Yukon Territory, 2006), making it difficult to account for the distribution patterns displayed by the returning salmon. In spite of this constraint, comparing the telemetry data from this study with large-scale basin features revealed several distinguishable patterns, with most fish returning to clear, moderately entrenched, upland rivers with moderate gradients and located in areas with modest relief. Although spawning often extended into the upper reaches of the tributaries, fish were generally absent in headwater areas, likely due to increased gradient and associated shifts in stream substrate and flow (as described by Church 2006).

Fish were generally absent in low-gradient reaches associated with floodplains and wide river valleys, areas typically characterized by marginally entrenched, meandering rivers and streams. This pattern was particularly apparent in the U.S. portion of the basin, where lowland reaches were more prevalent. All fish destined for Lower Yukon and Middle Yukon tributaries traveled to forested upland areas distinct from the Yukon River floodplain. Similarly, most spawning in the Tanana River drainage was concentrated in upland tributaries, with relatively few fish returning to the numerous low-gradient rivers flowing across the vast Tanana Flats, a glacial outwash plain characterized by broken forests and muskeg (Durst 2001). Fish returning to the Kantishna River (Tanana) and the Sheenjek and Chandalar rivers (the Yukon Flats) were notable exceptions, and further assessment of these area may provide additional insights into the factors associated with spawning site selection. Few fish returned to spawning areas in the Upper Koyukuk. The lower and middle reaches of this drainage flow through lowland flats associated with muskeg, off-channel sloughs, and broken timber. Chinook Salmon colonizing new areas may be less likely to make exploratory forays into relatively slow-moving, low-gradient rivers, even though their upper reaches may contain suitable spawning habitat. However, other limiting factors seem likely, since populations (once established) would presumably increase in abundance over time and expand into adjoining areas if suitable conditions were available.

Based on information from assessment projects within the basin (JTC 2002, 2004, 2005), it is often assumed that fish traveling farther upriver generally exhibit earlier run timing than those migrating shorter distances. Arriving earlier would

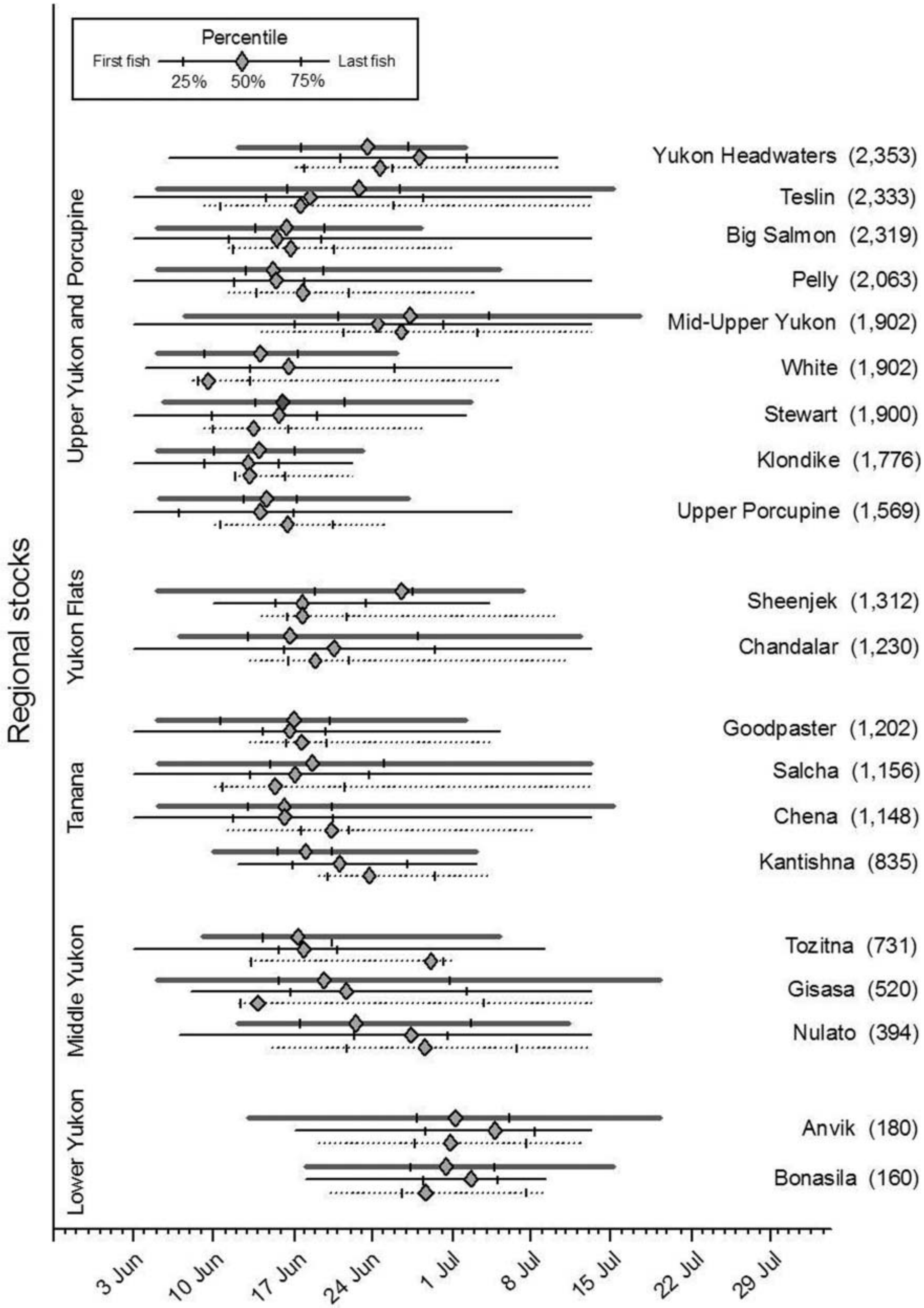

FIGURE 12. Lower-river run timing of Chinook Salmon stocks returning to terminal reaches of the Yukon River basin based on stock composition estimates of the return in 2002 (dotted lines), 2003 (thin solid lines), and 2004 (thick solid lines). The presence of the stock (first to last fish) and cumulative percentages (25th, 50th, and 75th percentiles) are indicated. The minimum distances from the tagging site to the terminal tributary tracking station are given in parentheses.

presumably provide additional time for these fish to reach spawning areas when conditions are optimal. However, the distribution of fish within the tributaries did not reflect this pattern, with comparable numbers of early- and late-run fish being distributed throughout the spawning areas. Although not surprising in small and medium-sized tributaries where the option of moving farther upriver is limited, this pattern was also observed in larger tributaries where spawning extended from near the tributary mouth to areas in excess of 500 km upriver. The Teslin River was the lone exception within the basin, with spatial and temporal differences in the spawning distribution of the fish. These differences were likely due to the added complexity of the drainage associated with Teslin Lake—a large lake system (120 km long and 5 km wide) located approximately 195 km upriver from the Yukon–Teslin River confluence—and the presence of extensive spawning areas both upriver and downriver from the lake. Although early-run fish spawned primarily in the upper reaches of the drainage, with some fish spawning over 500 km upriver from the tributary mouth, later-run fish spawned predominantly in the lower reaches downstream of the lake.

The status of the fish last located in nonterminal areas is uncertain, particularly those fish in U.S. reaches of the main stem. In addition to serving as a migratory corridor for fish traveling farther upstream, these areas potentially support local spawning populations. Main-stem spawning by Chinook Salmon has been reported in other large rivers, including the Sacramento River in California (Yoshiyama et al. 1998) and the Columbia River in Washington and Oregon (Chapman 1943; Swan 1989; Dauble and Geist 2000). Chapman (1943), describing observations in the Columbia River prior to dam construction, reported fish spawning in the main river channel at depths in excess of 4 m. More recent studies have located Chinook Salmon redds in water exceeding 6 m (Swan 1989). Main-stem spawning has been reported in Canadian reaches of the Upper Yukon (Milligan et al. 1985), although the extent was not determined due to turbid conditions. In addition to reports from local fishers, main-stem sampling late in the season (when fish in transit to tributaries farther upriver were not present) recovered fish in spawning condition.

Large-scale efforts to verify spawning activity in nonterminal reaches were not feasible during our study due to the turbid nature of the main stem, the scattered distribution of the fish, and the logistical difficulties associated with accessing and sampling the sites. However, there is suggestive evidence of main-stem spawning in the Upper Yukon. Most fish remaining in main-stem areas traveled to the upper reaches of the drainage, a pattern indicative of directed movements. A more random distribution would be expected if individuals were in a progressively weakened state and dying while in transit to areas farther upriver. Similarly, unreported fishery recoveries would be concentrated near local villages. In addition, the telemetry-based stock composition estimates for main-stem fish in the Upper Yukon were comparable to GSI estimates of the Canadian returns in 2008–2012 (P. A. Milligan, Department of Fisheries and Oceans Canada, unpublished data). The GSI estimates were based on untagged fish sampled near Eagle, Alaska, using the Canadian GSI baseline (updated in 2011) as a standard for stock allocation. The concordance between these two fundamentally different approaches not only provides suggestive evidence for the presence of main-stem spawning but also corroborates the information provided by our study and the methods used to obtain it. Only nominal information is available to suggest main-river spawning in the Tanana River. Most fish remaining in the main river returned to middle and upper reaches of the drainage. Some of the areas identified in the upper reaches were used later in the season by spawning Chum Salmon and may also represent Chinook Salmon spawning areas. Conversely, there was no ancillary information in the lower and middle reaches of the drainage, and unreported fishery recoveries may also account for fish last located in these areas.

It is unknown whether there is suitable salmon spawning habitat in U.S. reaches of the main stem. Spawning by other salmonids, including inconnu *Stenodus leucichthys*, whitefish *Coregonus* spp., and ciscoes *Coregonus* spp., has been reported in main-stem areas of the Yukon Flats (Brown et al. 2012), although these species are broadcast spawners and likely have different habitat requirements. Chinook Salmon last located in U.S. reaches may also have ultimately spawned in main-stem tributaries scattered along the water course; many of these tributaries were not surveyed due to the costs and logistical constraints. Based on our findings, fish returning to these tributaries would likely travel to upland reaches on the periphery of the Yukon River floodplain, which would simplify future survey efforts. A radio-tagged fish was serendipitously located during an overflight of the upper Hodzana River, a small main-stem tributary flowing into the Yukon Flats, suggesting that other main-stem tributaries may also support small spawning populations. Untagged Chinook Salmon have been reported in other small and medium-sized main-stem tributaries not surveyed during our study (Johnson and Daigneault 2008), although these sightings may also represent exploratory behavior exhibited by fish traveling farther upriver.

An alternative explanation is that nonterminal fish represent tagged individuals that died while in transit to upriver spawning areas due to the latent effects of handling, natural causes (e.g., disease, poor physical condition, or predation), injuries from encounters with fishing gear, or unreported fishery recoveries. The potential impacts associated with tagging effects are discussed below (see Tagging Response). Since the late 1990s, the fish parasite *Ichthyophonus* sp. has been reported in Yukon River Chinook Salmon, and sampling studies have suggested that infected fish destined for the Tanana River and upper basin may succumb to the parasite while in transit to spawning areas (Kocan and Hershberger 2006). While latent effects from handling and disease cannot be definitively ruled out, the migratory patterns of the fish suggest that these contributing factors do not fully explain the presence of fish in nonterminal areas. Slower swimming speeds would be expected for fish in the process of dying while in transit to areas farther upriver. However, most nonterminal fish did not exhibit this pattern, with only 30 individuals (1.5% of the tagged sample) exhibiting migration rates that were noticeably slower than those exhibited by fish harvested in fisheries or tracked to terminal tributaries in the Lower Yukon, Middle Yukon, and Yukon Flats (Eiler 2013).

The most likely explanation is that nonterminal fish represent undocumented fishery recoveries or fish that experienced fishery-related injuries. The migration rates of nonterminal fish were similar to those of fish harvested in main-stem fisheries. Although some nonterminal fish were located in isolated areas, most were concentrated near villages and fishing camps and often interspersed with confirmed fishery recoveries; a more random distribution would be expected for fish experiencing impaired swimming behavior from other causes. Physical injuries from encounters with fishing gear may also result in impaired swimming performance and undocumented mortality for fish within areas of intensive fishing pressure.

The importance of local support for research efforts is often underestimated. In the case of tagging studies, fishers are frequently reluctant to report tag recoveries due to the perception that the information will ultimately result in harvest restrictions or other unwanted management actions. In some remote communities, there is also a general distrust of outsiders and government programs. Extensive efforts were taken during this study to inform and encourage fishers to report tag recoveries. The success of this effort was obviously mixed, with substantial numbers of the tagged fish harvested but not reported. Some fishers reportedly threw transmitters back in the river, further confounding efforts to determine the status of the fish remaining in main-stem areas; only transmitters located out of water and in villages or fish camps were counted as unreported tag recoveries. The extent of this practice is unknown, making it difficult to assess its impact.

Ironically, several issues of interest to local fishers could have been addressed with an unambiguous assessment of fish status in main-stem areas. For example, the parasite *Ichthyophonus* is a major concern throughout the basin due to its effect on flesh quality and the potential impact on escapement vis-à-vis elevated mortality levels. Telemetry, in conjunction with accurate harvest information, provided an opportunity to address this issue by revealing the proportion of fish not completing their upriver migration due to non–fishery-related causes and the spatial distribution of these individuals. Future outreach efforts that emphasize how study results will be used to address local and basinwide concerns would likely increase the effectiveness of these programs. The findings from this study also demonstrate the importance of designing telemetry-based studies that incorporate independent assessments of fish status to confirm the integrity of the information collected.

Stock Composition

The composition of Yukon River Chinook Salmon returns varied substantially among regional areas and specific stocks. The runs were consistently dominated by Tanana and Upper Yukon stocks, which comprised over 70% of the annual return. Substantially fewer fish traveled to the other regional areas, ranging from less than 2% (Upper Koyukuk) to approximately 9% (the Yukon Flats) of the return. However, the collective contribution of these smaller aggregates was substantial, and management focusing only on the most prominent regional components could jeopardize a significant portion of the return.

The regional components of the returns typically consisted of several dominant stocks but also included a number of small, isolated populations. Upper Yukon returns were dominated by stocks returning to several prominent tributaries (the Stewart, Pelly, Big Salmon, and Teslin rivers) representing 60–63% of the regional return, with the remainder traveling to other scattered tributaries and main-stem reaches. This pattern was even more evident in the other regions. Fish returning to the Chena, Salcha, and Goodpaster rivers were the predominant Tanana stocks, comprising 80–90% of the regional return. Similarly, most fish returning to the Yukon Flats were destined for the Chandalar and Sheenjek rivers. Minor stocks were less prevalent in the other regions compared to the Upper Yukon. For example, although numerous rivers flow into the Tanana River, spawning populations were only located in a small number of isolated tributaries, suggesting that suitable spawning conditions were limited within this drainage.

Complex stock structures have been reported for Chinook Salmon in drainages throughout their range, including rivers in the Kamchatka Peninsula (Vronskiy 1972); Alaska and western Canada (Burger et al. 1985; Pahlke and Etherton 1999; Stuby 2007); and the Washington–California coast (Fulton 1968; Yoshiyama et al. 1998; Brannon et al. 2004). The composition of these returns may be even more complex than described, because the structure reported is often based on general in-river distribution, which tends to group fish by specific tributaries and may underestimate the underlying diversity. For example, Teslin River fish in the Upper Yukon exhibited spatial and temporal differences in distribution associated with geomorphic features within the drainage and potentially represent multiple stocks. Based on a finer scale of resolution, Chinook Salmon have been reported in over 110 spawning areas in Canadian reaches of the Upper Yukon (von Finster, unpublished). Keefer et al. (2004) noted that Chinook Salmon returns to major tributaries in the Columbia River were often considered single stocks even though other criteria suggested that more than one discrete spawning population was present.

Stock structure stability can have a major effect on how harvest regimes impact salmon returns and the effectiveness of conservation efforts. During our study, regional and stock composition estimates were remarkably similar across years, with notable differences being observed for only a few stocks. Conversely, abundance estimates during this period (2002–2004) indicated substantial annual variation in the magnitude of the run, with estimates of large Chinook Salmon (length >655 mm mideye to fork of tail) of 125,000, 262,000, and 230,000 fish based on mark–recapture experiments (Spencer et al. 2009) and 93,000, 245,000, and 110,000 fish based on lower-river sonar counts (JTC 2006). In spite of the sizable differences in the estimates (particularly in 2004), both methods indicated a substantial increase in run abundance during 2003. Other assessment projects in localized areas of the basin also reflected this trend (JTC 2006; Hayes et al. 2008). Combined with the stock composition estimates from our study, these findings suggest that annual changes in run abundance during 2002–2004 were not based on regional differences in abundance but were reflected in most of the regional and stock-specific components of the return.

Questions remain regarding the long-term stability of the composition of Chinook Salmon returns within the basin. Recent shifts in age composition to younger fish and reductions in fish size may reflect regional and stock-specific changes in stock structure. Genetic stock identification samples taken from test fisheries and in-river harvests are routinely used to characterize the stock composition of the return and typically categorize the run into lower-, middle-, and upper-basin components (Alaska Department of Fish and Game 2013). Additional research and assessments that examine stock composition in relation to the changing nature of the return would provide useful information for assessing management strategies and refining ongoing conservation efforts.

Run Timing

In spite of the extreme distances traveled by the fish (ranging from several hundred to several thousand kilometers upriver from the tagging area), the run timing exhibited by Yukon River Chinook Salmon was relatively compressed, with fish passing through the lower river during a 5–6-week period in late spring and early summer. Other rivers in western Alaska exhibit similar patterns, with run timing becoming progressively more protracted in drainages farther south along the western coast of North America (Burger et al. 1985; Department of Fisheries and Oceans 1999; Pahlke and Etherton 1999; Savereide 2005; Stuby 2007). In the southernmost portion of their range, Chinook Salmon returns extend throughout most of the year, with fish being classified into distinct spring–summer and fall runs (Fulton 1968; Healey 1991; Myers et al. 1998). Winter runs of Chinook Salmon also occur in the Sacramento River, with fish essentially passing through the lower river year-round (Yoshiyama et al. 1998). Even the spring–summer components in these southern rivers, which are analogous in many ways to the returns in Alaska and northwestern Canada, typically exhibit more protracted run timing than observed during our study. In the Columbia River, spring–summer Chinook Salmon pass through the lower river at Bonneville Dam over a 16–17-week period from early April through July (Keefer et al. 2004). Although less information is available on Chinook Salmon returns to rivers in the Russian Far East, run timing in the Kamchatka River typically ranges from late May to middle August (Vronskiy 1972).

Run timing differences within river basins have been reported for Chinook Salmon in relation to the distance traveled during the freshwater phase of their spawning migration, and management is often based on this temporal variation. In the Sacramento River, winter and spring Chinook Salmon generally travel to headwater reaches associated with higher elevations, whereas fall returns use spawning areas lower in the drainage (Yoshiyama et al. 1998). The timing of spring–summer Chinook Salmon in the Columbia River is strongly influenced by river discharge, with the proportion of lower-river stocks declining and upper-basin stocks increasing over the course of the run (Keefer et al. 2004). As previously mentioned, it is often assumed that Yukon River Chinook Salmon traveling farther upriver exhibit earlier run timing than those migrating shorter distances. However, in spite of the extreme disparity in distance traveled (ranging from several hundred to over 3,000 km), most Yukon River stocks were temporally similar. Tanana and Upper Yukon fish, the largest components of the return, exhibited similar peaks in abundance and substantial overlap in run timing. Timing differences were most distinct between stocks destined for the lower reaches of the Upper Yukon (early run) and Lower Yukon tributaries (late run), but even these stocks exhibited overlap in run timing.

The ostensive pattern within the basin (i.e., late-run fish traveling shorter distances) was further contradicted by the timing of fish traveling to headwater tributaries and nearby main-stem areas in the Upper Yukon. These fish traveled substantially farther than other stocks but exhibited extended run timing with fish continuing to pass through the lower river late in the return. The run timing exhibited by the fish presumably reflects adaptive behaviors that enhance spawning success in relation to the environmental conditions encountered. Although supportive evidence is not available for the Yukon River basin, the relatively compressed run timing exhibited by the fish indicates a narrow biological window in relation to the factors affecting the upriver migration, site selection, spawning activities, reproductive success, and juvenile survival.

Compared to rivers with more protracted returns, the short duration of the Yukon River run, combined with temporal similarities in lower-river passage, limits the usefulness of stock timing information for managing in-river fisheries. Marine and atmospheric conditions occasionally delay river entry by Yukon River Chinook Salmon (Mundy and Evenson 2011), which further compresses or shifts the overall run timing and can complicate management by increasing the overlap in the timing of regional and stock-specific components of the return. Despite these limitations, information from GSI sampling of in-river fisheries still provides important insights into run timing, particularly in relation to the passage and harvest of Canadian-origin stocks (Decovitch and Howard 2011). Timing differences could also be used to manage the harvest of lower-basin fish based on the later timing of these stocks. However, the magnitude of this component of the run is substantially less, and upper-basin fish are still passing through the lower river during this period (albeit at lower levels), limiting the utility of this approach. In addition, local fishers generally prefer to fish for Chinook Salmon earlier in the run due to reduced flesh quality as the run progresses and to ensure that adequate numbers of fish are harvested to meet their needs.

Validity of Stock Composition and Timing Estimates

An inherent limitation with telemetry data is that it most directly reflects the movements and behavior of the individuals within the tagged sample. Although sufficient for some research objectives, this information can be misleading when indiscriminately expanded to describe the associated population. The approach used during this study to estimate stock composition was designed to address bias related to temporal changes in abundance at the tagging site and to account for the disproportionate harvest of tagged fish traveling farther upriver. Although the regional distribution of the radio-tagged fish and the stock composition estimates derived from these data were generally similar (Figure 8), some differences were observed. The greatest disparity was observed for Upper Yukon fish, with differences between the two methods ranging from 3.7% in 2003 to 8.0% in 2002. Differences were even greater (9.3–13.1%) when fish remaining in nonterminal reaches were treated as in transit to areas farther upriver. Upper Yukon stocks traveled farther and were subjected to heavier fishing pressure over the course of the migration than fish returning to other regional areas, disproportionately increasing the number of tagged fish harvested and biasing stock composition estimates. Conversely, Tanana fish traveled shorter distances, were subjected to less fishing pressure, and showed negligible differences between sample proportions and stock composition estimates. Lower Yukon fish were exposed to substantially less fishing pressure, and sample percentages were somewhat higher than the stock composition estimates, particularly during 2002.

Tagging studies on migrating salmon often attempt to deploy tags in proportion to run abundance, relying on historical records or run timing estimates from assessment projects farther downriver. However, annual variation in timing and problems associated with the accuracy of in-season indices can frustrate these efforts. During our study, a general attempt was made to tag fish proportionally, but discrepancies periodically occurred. For example, a disproportionate number of fish were tagged late in the run during 2002 (Figure 3), which tended to underestimate upper-basin stocks with earlier run timing and inflate estimates of later-run stocks. Lower Yukon fish, which were more prevalent later in the run, comprised 13% of the tagged sample, compared with 6% of the return based on stock composition estimates. Random or selective sampling (e.g., tagging every third fish captured) has been used to account for temporal differences, alleviating some of these limitations (Johnson et al. 1993; Savereide 2005). However, this approach may be biased (when changing river conditions alter fishing efficiency) or impractical (when there are problems capturing adequate numbers of fish). The model developed during this study did not depend on strict proportional tagging, eliminated the need to subsample the fish captured, and addressed the problems associated with disproportionate harvests of tagged individuals during their upriver migration.

Capture and tagging efforts during our study were sufficient to obtain fairly inclusive samples of the component stocks. In addition to the major segments of the return, minor stocks scattered throughout the basin were consistently represented (e.g., from fish returning to the Innoko River in the lower basin to Tatchun Creek in the upper headwaters). The population of some of these stocks was relatively small. Fish returning to Beaver Creek in the Yukon Flats were identified as a component stock during all 3 years of the study. Fewer than 200 Chinook Salmon were counted at an enumeration weir on this tributary during 1999–2000 (Collin et al. 2002). Stocks known to be major components of the return, based on other assessment projects within the basin, were also well represented by the telemetry-based estimates. For example, Chinook Salmon returning to the Chena and Salcha rivers reportedly have some of the largest escapements within the U.S. portion of the basin (Schultz et al. 1994), a finding similar to our results.

Stock composition estimates were based on the premise that fish in designated stock groups represented local spawning populations. Fidelity to natal rivers was strong during the study, and fish that traveled to terminal tributaries were assumed to have reached their final destination. The status of fish in nonterminal reaches was less certain because these fish may represent individuals that died while in transit to areas farther upriver as well as fish spawning locally. Stock composition estimates that treated in-transit fish as local spawners would underestimate the contribution of stocks traveling farther upriver, whereas estimates that assumed that all nonterminal fish were in transit (i.e., treated as fishery recoveries) could overestimate the contribution of upriver stocks. Although definitive information on the status of nonterminal fish is not available, an analysis of the distribution and final location of these individuals suggests that nonterminal reaches likely included both in-transit and spawning fish. Separate composition estimates based on both extremes (i.e., all nonterminal fish spawning locally versus all nonterminal fish in transit), were reasonably similar, suggesting that there is minimal bias related to the treatment of nonterminal fish. The actual composition of the returns is likely between these two estimates.

The accuracy of stock composition estimates is particularly important in the Yukon River basin, since information on country of origin is needed to assess conservation efforts and harvest allocations between the United States and Canada. We used Upper Yukon fish to represent the Canadian contribution, since most (99%) were destined for Canadian reaches of the basin. In general, our country-of-origin estimates were consistent with other estimates reported for the basin. Scale pattern analysis from the early 1980s suggested that Canadian-origin fish in the Upper Yukon comprised between 42% and 54% of the return (unpublished report on the status of salmon stocks, fisheries, and management programs in the Yukon River prepared by the Scientific Working Group for the delegations from the United States and Canada concerning the Yukon River, April 23–24, 1985). Based on catch and escapement information in the early 1980s, Milligan et al. (1985) estimated that approximately 50% of the return was made up of Canadian stocks, ranging from 44–51% in years with low returns to 48–57% in years of greater abundance. Genetic stock identification estimates of the Canadian contribution from 1987 to 1990 averaged 53%, ranging from 42% to 61% of the return (Wilmot et al. 1992). Not all stocks were included in the GSI baseline used in that study, most notably fish returning to spawning areas in the Yukon Flats, which undoubtedly biased these estimates to some extent. Additional sampling was subsequently conducted in the basin using the 2002–2004 telemetry data to enhance the GSI baseline (Templin et al. 2006; Flannery et al. 2012). Based on the updated information, the seasonal composition trends determined from mixed-stock fisheries in the lower Yukon River during 1987–1990 and 2002–2003 (Templin et al. 2005) were similar to those observed during our study. Conversely, lower contribution estimates have been proposed based on GSI sampling in the lower Yukon River during 2005–2011, with the Canadian contribution averaging around 40% of the return (Hamazaki and DeCovitch 2014).

Sampling methods may partially explain some of the discrepancies in the country of origin estimates reported. Because of the size selectivity of larger-mesh gill nets (Fujimori and Tokai 2001; Fukuwaka et al. 2008), we assume that the length frequency of our tagged sample was not representative of the entire run. Smaller fish (i.e., 3- and 4-year-olds), which made up 4.1% of the tagged sample, were likely underrepresented and the composition estimates obtained more reflective of the older fish. However, the significance of this bias is unclear since definitive information on regional and stock-specific size and age composition is not readily available due to logistical constraints within the basin and the resulting assortment of sampling methods used (ranging from gill nets and fish wheels in main-river areas to weirs, aerial surveys, and carcass sampling in some terminal tributaries). Since the mid-1980s, older fish (i.e., 5-year-olds and older) were generally considered the primary component of the return. Basinwide estimates of younger fish derived from test gill-net fisheries near the river mouth during 1985–2010 averaged only 2.1% of the run (Schumann and Dubois 2012). However, higher proportions of younger fish have been reported for minor stocks returning to several small and medium-sized tributaries with weirs in the lower and middle basin. For example, the percentage of younger fish returning to the Andreafsky River, which is located 160 km from the mouth of the Yukon River, ranged from 3.0% to 48.8% annually (Tobin and Harper 1998; Maschmann 2009). Unfortunately, due to logistical constraints, comparable data are not available in larger tributaries with greater flows and larger numbers of fish.

Biased sampling related to size and age differences would have less of an impact if regional and stock-specific components of the run were similar (i.e., consistent bias across stocks). Based on information from regional assessment projects (Schumann and DuBois 2012) and the perception that smaller fish would be less capable of making the extended migrations farther upriver, it is generally believed that average size tends to be less for fish returning to spawning areas in the lower basin, which would suggest that our composition estimates for lower-basin stocks were biased low. However, the disparity in size and age structure among the regional and stock-specific components of the run is not known. In addition to sampling issues in the lower basin, assessment efforts in the upper basin are generally limited to sonar counts, fish wheels, and fishery sampling in main-stem reaches and to aerial surveys, sonar counts, and carcass sampling in terminal tributaries (JTC 2013). Although instructive, these projects do not provide comprehensive information on age and size structure. Few weirs are operated in the upper basin, and the data are typically limited to fish counts (E. MacDonald, Department of Fisheries and Oceans Canada, personal communication).

Despite the lack of definitive information, there was general agreement between our stock composition and timing estimates and those of other assessment projects within the basin. Large numbers of Chinook Salmon are visually counted from counting towers on the Chena and Salcha rivers (Schultz et al. 1994). Although these counts are considered minimum estimates due to periodically high water and poor viewing conditions (Doxey et al. 2005), the general timing patterns for radio-tagged fish (based on station records) and untagged fish (based on the visual counts) were similar.

There was also general agreement between our composition estimates for Upper Yukon stocks and those based on GSI sampling at fish wheels near the U.S.–Canada border during 2005–2007 (Beacham and Candy 2006, 2007, 2008). For example, our estimates of Stewart River fish ranged from 8% to 14% of the Canadian return (4–7% of the entire return), compared with GSI estimates of 9–14%. Similar patterns were observed for the other major stocks, including the Pelly River (18–20% versus 12–21%), Big Salmon River (10–15% versus 10–11%), and Teslin River stocks (19–20% versus 13–19%). Minor stocks showed less agreement. Estimates for the Klondike River (3–5% versus 2–4%) and Nordenskiold River stocks (1–2% versus $\leq$1%) were comparable, whereas those for the White River (3–8% versus 1–2%) and Chandindu River stocks (2–4% versus 7–8%) were more disparate. The GSI estimates for the Chandindu River were substantially higher than is credible, likely due to sampling bias related to the proximity of this tributary to the fish wheels and associated bank orientation of the fish (P. Milligan, Department of Fisheries and Oceans Canada, personal communication).

Less information is available on the abundance and timing of Chinook Salmon stocks in the Lower Yukon, with most assessment efforts in terminal tributaries being limited to the enumeration weir on the Andreafsky River (downriver from the study area) and carcass sampling and periodic aerial surveys in the Anvik River (Sandone 1994; Templin et al. 2006). Although not particularly instructive, the spawning distribution of radio-tagged fish in the Anvik River conformed to local information for this tributary.

The general pattern of agreement between our study and other fundamentally different assessment projects within the basin suggests that the telemetry-based stock composition and timing estimates provided a plausible approximation of the 2002–2004 returns, particularly for the larger stock groups. Although questions remain regarding potential sampling bias in relation to the size and age structure of the run, the telemetry-based estimates are still informative, particularly when considering the older component of the return. However, the short duration of the run, its complex stock structure, and the temporally similar stock timing of the return complicates Chinook Salmon management and conservation efforts within the basin.

Tagging Response

A basic assumption of any tagging study is that the capture and handling methods do not adversely affect the fish (i.e., tagged fish behave the same as untagged fish) or that any effect is limited in severity and duration and ultimately has negligible impact. In the case of migrating salmon, procedures that violate these assumptions undoubtedly affect upriver movements and in extreme cases may even alter the final destination of the fish, underscoring the need to evaluate the response exhibited after release to validate the veracity of the data. Most of the fish we tagged resumed upriver movements, which suggests minimal tagging effect. The percentage of fish that did not move upriver (2–3% annually) was comparable to or lower than that reported for salmon telemetry studies in other rivers (e.g., Burger et al. 1985; Matter and Sandford 2003; Keefer et al. 2004).

However, capture and handling methods can have a variety of effects on fish, ranging from minimal impact to impaired behavior, exhaustion, and death. In addition to physical injury, the stress experienced by the fish can be a major factor and can have an immediate or latent effect on swimming performance (Schreck 1981, 2000, 2010), behavior (Schreck et al. 1997), and reproductive success (Schreck et al. 2001; Schreck 2010). Sublethal effects may also increase the vulnerability of the fish to other limiting factors, such as adverse environmental conditions, increased performance demands, and the associated allostatic loads (Schreck 1981, 2010)—factors that are likely experienced by salmon during the upriver migration due to the extended distances traveled, the catabolic state of the fish, and the need to avoid predation and compete with other individuals after reaching spawning areas. Budy et al. (2002) speculated that the cumulative effects of stress may be delayed for some time due to the complex interactions with other potential sources of mortality.

Latent and sublethal effects are often difficult to assess, particularly in large remote river drainages where access to the fish is limited. Radio-tagged fish that stop moving and die soon after release are relatively easy to identify, whereas impaired movements upriver are more difficult to distinguish, particularly when the final destination and normal patterns of movement are not known and may be the primary study objective. Furthermore, the severity of the effect may be influenced by a number of factors, including the capture and tagging methods used; environmental conditions; and the maturity, physical condition, and size of the fish (Bridger and Booth 2003). Fish experiencing latent or sublethal tagging effects presumably exhibit reduced vitality and impaired movements as they move upriver. The actual response would likely be expressed as slower than normal migration rates, migratory patterns exhibiting an accelerated decline in swimming speed, or truncated movements (i.e., atypical distribution). Fish traveling extended distances would be particularly susceptible to latent and sublethal effects.

Due to logistical constraints, most of the research related to the tagging effects displayed by salmon has focused on laboratory studies of surgically tagged juveniles. Jepsen et al. (2002) reported that cortisol levels (an indicator of stress) in juvenile Chinook Salmon increased substantially and remained elevated for 24–48 h after tagging, whereas fish that were only handled returned to pretrauma levels within several hours. These findings also suggest that the effects from the tagging were short term, with tagged fish returning to normal cortisol levels within several days. Tagged and untagged Atlantic salmon *Salmo salar* smolts exhibited comparable swimming speeds during controlled endurance tests, although performance was influenced by fish and transmitter size (McCleave and Stred 1975). Conversely, Adams et al. (1998) reported adverse impacts on swimming performance for juvenile Chinook Salmon 21 d after tagging, but fish size and the methods used were again contributing factors.

Although in situ studies are less definitive due to inherent limitations in interpreting the results, such studies can provide useful insights on the tagging effects exhibited by adult salmon. Stress indicators, including elevated cortisol, lactate, and glucose levels, were related to lower return rates for Fraser River Sockeye Salmon *O. nerka* tagged during the marine phase of their spawning migration (Cooke et al. 2006). Decreasing tagged–untagged ratios in upriver recovery areas were observed for spaghetti-tagged Chum Salmon during mark–recapture studies on the Yukon River, suggesting that capture and handling increased mortality rates (Bromaghin et al. 2007). During a companion study, radio-tagged Chum Salmon handled in the same manner (i.e., held in fish wheel live boxes for several hours prior to tagging) exhibited delayed upriver movements and slower migration rates than fish that were radio-tagged and released immediately after capture, suggesting that the stress associated with being held negatively affected the response exhibited by the fish (Eiler, unpublished report). Comparisons of adult Chinook Salmon tagged with passive integrated transponder tags and fish implanted with radio transmitters in the lower Columbia River found no evidence that radio-tagging adversely affected migratory behavior and upriver movements (Matter and Sandford 2003). The wide range of responses reported by these and other studies is not particularly surprising considering the diverse set of circumstances and conditions involved, including differences in river characteristics, species tagged, fish characteristics (life stage, physical features, and condition), and the capture, handling, and tagging methods used.

Although the fish in our study responded well to the capture, handling, and tagging methods used (with 97.5% resuming upriver movements), there is evidence that they initially displayed a negative tagging effect. Migration rates between the tagging area and Paimiut were significantly slower than in reaches immediately upriver. Chinook Salmon within the basin generally exhibited a progressive decline in migration rate as they moved upriver and neared their natal streams, with increases in swimming speed typically associated with major changes in the physical features of the basin (Eiler 2013). River characteristics from the tagging area to the Yukon–Anvik River confluence were similar, suggesting that the slower migration rates exhibited by the fish immediately after release were likely tagging induced.

Differences in migration rates at Paimiut and the Yukon–Anvik River confluence also showed that fish tagged farther downstream (i.e., fish that had traveled greater distances after release) were swimming considerably faster and were progressively less variable as they moved upriver past the station sites, suggesting that these individuals had recovered more fully and were beginning to exhibit more normal swimming behavior. These findings suggest that although the tagging effect was relatively widespread, with some individuals still exhibiting residual effects 200 km upriver from their release site, it was relatively short in duration (several days) and less influential over time. Caution is obviously needed when assessing movement data from tagging studies due to the potential bias associated with tagging effect. During this study, we censored information downstream of Paimiut when estimating migration rates to address concerns that the fish were not exhibiting normal swimming behavior (Eiler 2013).

It is not definitely known whether the reduced migration rates exhibited by the fish immediately after release represented a reduction in swimming speed or an aberrant migratory pattern. Limited fine-scale tracking from boats near Russian Mission determined that at least some fish remained in main-stem eddies for several hours after tagging (presumably recovering from the procedure), although other fish resumed upriver movements immediately after release. A similar pattern was also observed just upriver from the tagging area, with fish holding in quiet water (e.g., eddies and downstream ends of islands), although it is not known whether this reflected normal migratory behavior or was an artifact of the tagging effect. Other salmon telemetry studies have reported interrupted movements after tagging, with fish dropping downstream or temporarily delaying their upriver migration after tagging (Gray and Haynes 1979; Burger et al. 1985; Bernard et al. 1999).

The fish in our study did not exhibit the upriver migratory patterns typically associated with latent or sublethal tagging effects. The migration rates of fish returning to the upper basin were remarkably fast considering the distances traveled (thousands of kilometers), ranging from 52 to 62 km/d (Eiler 2013). By comparison, Chinook Salmon in main-stem reaches of the Columbia River averaged around 35 km/d (Keefer et al. 2004; Goniea et al. 2006). Although Yukon River Chinook Salmon exhibited a general decline in migration rate as they moved upriver and neared their spawning areas, the migratory patterns varied between reaches and were more reflective of changes in river characteristics than impaired swimming behavior (Eiler 2013). As previously mentioned, the fish remaining in nonterminal areas may represent mortalities associated with latent tagging effects, but the proximity of these fish to local fisheries and the movement patterns exhibited prior to arriving at their final locations suggest that other factors may better explain their presence in these areas.

Several indirect measures also support the assumption that the upriver movements observed during this study were comparable to normal, nonimpaired migratory patterns. Information on the timing of distinct pulses of Chinook Salmon harvested in village fisheries along sequential reaches of the main stem suggests that untagged fish were traveling between 48 and 56 km/d (T. Vania, Alaska Department of Fish and Game, personal communication), migration rates similar to those of the radio-tagged fish. Similarly, Chinook Salmon radio-tagged at Rapids (Figure 1) in 1998 traveled an average of 53 km/d during their upriver migration (JTC 1998). These rates are comparable to those observed for upper-basin fish tagged during our study, even though the fish tagged at Russian Mission traveled substantially farther after being released. Additionally, there was a high degree of concordance between Chinook Salmon sonar counts in the Big Salmon River (which is located in the upper headwaters of the basin; Figure 1) during 2005 and the composite timing (2002–2004) of radio-tagged fish passing the tracking station near the river's mouth. The dates of the arrival of the first and last fish, the peak counts, and the 90% cumulative counts for both methods were within a couple days of each other (Mercer and Wilson 2005).

Similar observations were made at assessment projects on the main stem (e.g., test fish wheels located at Rapids) and in major spawning tributaries, with the radio-tagged fish mirroring the timing of untagged fish.

Schreck (2000) suggested that the impact of stress on swimming performance and survival is dependent on the severity, duration, and frequency of the stress experienced by the fish. The physical nature and severity of capture- and handling-related injures will undoubtedly influence the immediate and long-term response as well. To address these concerns, a number of steps were taken during our study to minimize physical injuries and handling-induced stress to the fish. The gill nets used to capture the fish were constructed with cable laid netting instead of monofilament to minimize injuries and make it easier to remove the fish from the mesh. The mesh was cut to further facilitate removal. The relatively short nets and the fishing methods employed (e.g., retrieving the nets as soon as fish were detected and retaining only two fish per set regardless of the number caught) undoubtedly reduced the number of fish captured and tagged. However, these methods substantially reduced the time needed to process the catch and thus likely reduced the stress experienced by the fish. Capture and handling methods can have a major impact on tagging response. In an extreme case, steelhead *O. mykiss* were captured and radio-tagged as a sample of opportunity in a Sockeye Salmon test fishery using standard fishing methods (i.e., large, commercial gill nets fished for 1-h periods). Only 49 (43%) of the 113 steelhead captured were judged to be in suitable condition for tagging, and only 8 of these moved upriver after release (Beere 1991), further illustrating the importance of handling issues.

Technical aspects of tagging, such as transmitter size and attachment methods, can also have considerable impact on how tagged fish behave after release. Several recent review articles discuss these issues in detail (Bridger and Booth 2003; Liedtke and Rub 2012). The tagging equipment and techniques used during this study were based on methods used successfully in previous salmon studies in large rivers (Eiler 1990, 1995; Eiler et al. 1992), and the results from the current study suggest that these methods were relatively benign.

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Appendix: Detailed Data

TABLE A.1. Regional distribution of Chinook Salmon radio-tagged in the lower Yukon River basin during 2002–2004. Fish harvested in terminal regions are listed. Individuals harvested in terminal tributaries were considered to have reached their final destination. The percentages of the annual totals are given in parentheses.

Region	Final location	2002	2003	2004	All years
Lower Yukon	Yukon tributaries	49 (9.4)	39 (4.5)	59 (8.1)	147 (6.9)
	Yukon River[a]	2 (0.4)	1 (0.1)	21 (2.9)	24 (1.1)
	Combined areas	51 (9.8)	40 (4.6)	80 (11.0)	171 (8.1)
Middle Yukon	Yukon tributaries	32 (6.1)	39 (4.5)	33 (4.6)	104 (4.9)
	Yukon River[a]	19 (3.6)	41 (4.7)	37 (5.1)	97 (4.6)
	Combined areas	51 (9.8)	80 (9.1)	70 (9.7)	201 (9.5)
Upper Koyukuk	Koyukuk tributaries	5 (1.0)	14 (1.6)	17 (2.3)	36 (1.7)
	Koyukuk fisheries	1 (0.2)	4 (0.5)	3 (0.4)	8 (0.4)
	Combined areas	6 (1.2)	18 (2.1)	20 (2.8)	44 (2.1)
Tanana	Tanana tributaries	103 (19.8)	159 (18.2)	144 (19.9)	406 (19.2)
	Tanana River	6 (1.2)	12 (1.4)	28 (3.9)	46 (2.2)
	Tanana fisheries	9 (1.7)	19 (2.2)	22 (3.0)	50 (2.4)
	Combined areas	118 (22.6)	190 (21.7)	194 (26.8)	502 (23.7)
Yukon Flats	Yukon tributaries	30 (5.8)	60 (6.9)	24 (3.3)	114 (5.4)
	Yukon River[a]	26 (5.0)	31 (3.5)	23 (3.2)	80 (3.8)
	Combined areas	56 (10.7)	91 (10.4)	47 (6.5)	194 (9.2)
Upper Porcupine	Porcupine tributaries	11 (2.1)	27 (3.1)	9 (1.3)	47 (2.2)
	Porcupine fisheries	1 (0.2)	4 (0.4)	3 (0.4)	8 (0.4)
	Combined areas	12 (2.3)	31 (3.5)	12 (1.7)	55 (2.6)
Upper Yukon	Yukon tributaries	139 (26.7)	323 (36.9)	199 (27.5)	661 (31.2)
	Yukon River[a]	55 (10.6)	74 (8.5)	56 (7.7)	185 (8.7)
	Canadian fisheries[b]	33 (6.3)	28 (3.2)	46 (6.4)	107 (5.0)
	Combined areas	227 (43.6)	425 (48.6)	301 (41.6)	953 (45.0)
Total		521	875	724	2,120

[a]Main-stem reaches, including associated tributaries, that were not monitored by means of tracking stations or aerial surveys.

[b]Includes fish caught in the U.S. fishery near Eagle, Alaska.

TABLE A.2. Stock-specific distribution of Chinook Salmon radio-tagged in the lower Yukon River basin during 2002–2004. Fish harvested in terminal tributaries were considered to have reached their final destination. The percentages of the annual totals are given in parentheses.

Region	Stock	2002	2003	2004	All years
Lower Yukon	Anvik	34 (7.1)	31 (3.8)	40 (6.2)	105 (5.4)
	Bonasila	10 (2.1)	6 (0.7)	14 (2.2)	30 (1.5)
	Innoko	5 (1)	2 (0.2)	5 (0.8)	12 (0.6)
	Yukon River[a]	2 (0.4)	1 (0.1)	21 (3.2)	24 (1.2)
	Combined areas	51 (10.7)	40 (5.0)	80 (12.3)	171 (8.8)
Middle Yukon	Nulato	19 (4.0)	15 (1.8)	11 (1.7)	45 (2.3)
	Gisasa[b]	4 (0.8)	11 (1.3)	8 (1.2)	23 (1.2)
	Kateel[b]	1 (0.2)			1 (0.1)
	Melozitna	1 (0.2)	1 (0.1)	3 (0.5)	5 (0.3)
	Nowitna	1 (0.2)	2 (0.2)	3 (0.5)	6 (0.3)
	Tozitna	6 (1.3)	10 (1.2)	8 (1.2)	24 (1.2)
	Yukon River[a]	19 (4.0)	41 (5.0)	37 (5.7)	97 (5.0)
	Combined areas	51 (10.7)	80 (9.8)	70 (10.8)	201 (10.3)
Upper Koyukuk	Koyukuk River	5 (1.0)	7 (0.9)	10 (1.5)	22 (1.1)
	Hogatza		1 (0.1)		1 (0.1)
	Henshaw		1 (0.1)	2 (0.3)	3 (0.2)
	South Fork		3 (0.4)	5 (0.8)	8 (0.4)
	Middle Fork		2 (0.2)		2 (0.1)
	Combined areas	5 (1.0)	14 (1.7)	17 (2.6)	36 (1.8)
Tanana	Lower Tanana River[a]	2 (0.4)	2 (0.2)	8 (1.2)	12 (0.6)
	Kantishna	8 (1.7)	15 (1.8)	9 (1.4)	32 (1.6)
	Tolovana	2 (0.4)	5 (0.6)	5 (0.8)	12 (0.6)
	Nenana		3 (0.4)	1 (0.2)	4 (0.2)
	Middle Tanana River[a]	3 (0.6)	4 (0.5)	12 (1.8)	19 (1.0)
	Clear			3 (0.5)	3 (0.2)
	Chena	30 (6.3)	40 (4.9)	30 (4.6)	100 (5.1)
	Moose		1 (0.1)		1 (0.1)
	Salchaket		1 (0.1)		1 (0.1)
	Salcha	47 (9.9)	58 (7.1)	68 (10.5)	173 (8.9)
	Upper Tanana River[a]	1 (0.2)	6 (0.7)	8 (1.2)	15 (0.8)
	Goodpaster	16 (3.4)	36 (4.4)	28 (4.3)	80 (4.1)
	Combined areas	109 (22.9)	171 (20.9)	172 (26.5)	452 (23.2)
Yukon Flats	Beaver	1 (0.2)	3 (0.4)	2 (0.3)	6 (0.3)
	Hodzana			1 (0.2)	1 (0.1)
	Chandalar	15 (3.1)	35 (4.3)	14 (2.2)	64 (3.3)
	Sheenjek	12 (2.5)	20 (2.4)	6 (0.9)	38 (2.0)
	Black	2 (0.4)	2 (0.2)	1 (0.2)	5 (0.3)
	Yukon River[a]	26 (5.5)	31 (3.8)	23 (3.5)	80 (4.1)
	Combined areas	56 (11.7)	91 (11.1)	47 (7.2)	194 (10.0)
Upper Porcupine	Coleen			3 (0.5)	3 (0.2)
	U.S. tributaries	3 (0.6)		1 (0.2)	4 (0.2)
	Old Crow River		2 (0.2)	1 (0.2)	3 (0.2)
	Porcupine River (Can)[c]	5 (1.0)	10 (1.2)	1 (0.2)	16 (0.8)
	Whitestone[c]		1 (0.1)		1 (0.1)
	Miner[c]	3 (0.6)	14 (1.7)	3 (0.5)	20 (1.0)
	Combined areas	11 (2.3)	27 (3.3)	9 (1.4)	47 (2.4)

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TABLE A.2. Continued.

Region	Stock	2002	2003	2004	All years
Upper Yukon	Charley	2 (0.4)	3 (0.4)	1 (0.2)	6 (0.3)
	Kandik	1 (0.2)	1 (0.1)		2 (0.1)
	Nation		2 (0.2)	2 (0.3)	4 (0.2)
	Chandindu[c]	1 (0.2)	5 (0.6)	1 (0.2)	7 (0.4)
	Klondike[c]	6 (1.3)	19 (2.3)	12 (1.8)	37 (1.9)
	Sixtymile[c]			1 (0.2)	1 (0.1)
	Stewart[c]	21 (4.4)	30 (3.7)	26 (4.0)	77 (4.0)
	White[c]	8 (1.7)	12 (1.5)	12 (1.8)	32 (1.6)
	Pelly[c]	32 (6.7)	79 (9.6)	48 (7.4)	159 (8.2)
	Below Yukon-Pelly[a,c]	13 (2.7)	13 (1.6)	14 (2.2)	40 (2.1)
	Above Yukon-Pelly[a,c]	42 (8.8)	61 (7.4)	42 (6.5)	145 (7.4)
	Big[c]		1 (0.1)		1 (0.1)
	Tatchun[c]	4 (0.8)	3 (0.4)	3 (0.5)	10 (0.5)
	Nordenskiold[c]	2 (0.4)	8 (1.0)	2 (0.3)	12 (0.6)
	Little Salmon[c]	2 (0.4)	17 (2.1)	3 (0.5)	22 (1.1)
	Big Salmon[c]	17 (3.6)	59 (7.2)	25 (3.8)	101 (5.2)
	Teslin[c]	36 (7.5)	71 (8.7)	49 (7.5)	156 (8.0)
	Hootalinqua[c]	7 (1.5)	7 (0.9)	9 (1.4)	23 (1.2)
	Takhini[c]		6 (0.7)	5 (0.8)	11 (0.6)
	Combined areas	194 (40.7)	397 (48.4)	255 (39.2)	846 (43.5)
Total		477	820	650	1,947

[a]Reaches of the Yukon River main stem, including associated tributaries, that were not monitored by means of tracking stations or aerial surveys.
[b]Tributaries in the lower reaches of the Koyukuk River.
[c]Canadian reaches of the basin.

TABLE A.3. Stock composition estimates of Chinook Salmon returns in 2002–2004 based on the distribution of radio-tagged fish weighted by catch per unit effort information at the tagging site and adjusted for the harvests of tagged individuals in upriver fisheries. The percentages of the return and the 95% confidence intervals (in parentheses) are shown.

Region	Stock	2002	2003	2004
Lower Yukon	Innoko	0.7 (0.1, 1.4)	0.2 (0.0, 0.5)	0.5 (0.1, 1.0)
	Bonasila	0.9 (0.4, 1.5)	0.4 (0.1, 0.8)	1.5 (0.7, 2.3)
	Anvik	3.0 (2.0, 4.1)	2.6 (1.8, 3.5)	4.1 (2.9, 5.6)
	Yukon River[a]	2.9 (1.5, 4.5)	4.4 (3.2, 5.7)	5.7 (4.1, 7.4)
Middle Yukon	Nulato	1.9 (1.0, 2.8)	1.3 (0.7, 2.0)	1.7 (0.7, 2.8)
	Gisasa	0.3 (0.1, 0.6)	1.0 (0.4, 1.6)	0.8 (0.3, 1.4)
	Lower Koyukuk[a]	0.1 (0.0, 0.3)		0.7 (0.2, 1.3)
	Melozitna	0.1 (0.0, 0.5)	0.1 (0.0, 0.3)	0.3 (0.0, 0.7)
	Nowitna	0.2 (0.0, 0.8)	0.2 (0.0, 0.5)	0.4 (0.0, 1.0)
	Tozitna	1.2 (0.4, 2.3)	1.1 (0.4, 1.8)	1.0 (0.4, 1.8)
	Yukon River[a]	0.8 (0.3, 1.4)	0.8 (0.3, 1.5)	1.5 (0.7, 2.3)
Upper Koyukuk	Upper tributaries[b]	1.1 (0.2, 2.2)	1.9 (1.0, 2.8)	1.7 (0.9, 2.7)
Tanana	Main river (lower)[a]	0.2 (0.0, 0.6)	0.2 (0.0, 0.5)	0.9 (0.3, 1.7)
	Kantishna	1.1 (0.4, 2.0)	1.4 (0.8, 2.2)	1.2 (0.5, 2.0)
	Tolovana	0.4 (0.0, 1.1)	0.5 (0.1, 1.0)	0.6 (0.1, 1.3)

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TABLE A.3. Continued.

Region	Stock	2002	2003	2004
	Main river (middle)[a]	0.3 (0.0, 0.8)	0.7 (0.2, 1.2)	1.3 (0.5, 2.2)
	Chena	5.3 (3.4, 7.5)	4.8 (3.4, 6.2)	4.3 (2.8, 5.9)
	Salcha	10.7 (7.5, 14.2)	6.4 (4.9, 8.0)	10.1 (7.9, 12.4)
	Main river (upper)[a]	0.1 (0.0, 0.4)	1.0 (0.4, 1.6)	2.2 (1.2, 3.5)
	Goodpaster	2.8 (1.5, 4.5)	4.4 (3.0, 5.8)	3.6 (2.4, 5.0)
Yukon Flats	Main stem (lower)[a,c]	0.1 (0.0, 0.4)	2.5 (1.5, 3.6)	2.8 (1.7, 4.2)
	Beaver	0.1 (0.0, 0.4)	0.3 (0.0, 0.8)	0.4 (0.0, 1.0)
	Chandalar	3.4 (1.9, 5.2)	4.0 (2.8, 5.4)	1.7 (0.9, 2.8)
	Sheenjek	2.5 (1.2, 4.2)	2.4 (1.4, 3.4)	1.0 (0.3, 1.9)
	Black	0.4 (0.0, 1.1)	0.2 (0.0, 0.6)	0.1 (0.0, 0.3)
	Main stem (upper)[a,d]	0.3 (0.0, 0.8)	1.2 (0.5, 2.0)	0.4 (0.0, 0.8)
Upper Porcupine	U.S. tributaries	0.6 (0.0, 1.6)		0.8 (0.2, 1.5)
	Upper tributaries[e]	2.7 (1.0, 4.7)	3.9 (2.6, 5.3)	1.3 (0.5, 2.4)
Upper Yukon	Charley	0.3 (0.0, 0.9)	0.4 (0.0, 0.8)	0.2 (0.0, 0.5)
	Kandik-Nation	0.6 (0.0, 2.2)	0.3 (0.0, 0.7)	0.3 (0.0, 0.9)
	Main stem (lower)[a]	1.8 (0.6, 3.4)	0.9 (0.3, 1.6)	0.9 (0.2, 1.8)
	Klondike[e]	1.6 (0.5, 3.2)	2.5 (1.5, 3.7)	2.0 (1.0, 3.1)
	Main stem (middle)[a]	3.8 (2.2, 5.8)	4.3 (3.0, 5.7)	4.8 (3.2, 6.5)
	Stewart[e]	7.2 (4.0, 10.3)	4.2 (2.9, 5.7)	4.7 (3.0, 6.5)
	White[e]	4.0 (0.9, 7.9)	1.6 (0.8, 2.5)	2.2 (1.1, 3.4)
	Pelly[e]	9.2 (6.2, 12.6)	10.0 (8.0, 12.1)	9.4 (7.1, 11.8)
	Tatchun[e]	0.7 (0.1, 1.6)	0.3 (0.0, 0.6)	0.4 (0.0, 1.0)
	Main stem (upper)[a]	4.9 (3.1, 6.9)	4.4 (3.0, 5.8)	5.3 (3.6, 7.1)
	Nordenskiold[e]	0.7 (0.0, 1.9)	1.2 (0.5, 2.1)	0.3 (0.0, 0.8)
	Little Salmon[e]	0.2 (0.0, 0.9)	2.1 (1.2, 3.2)	0.4 (0.0, 0.9)
	Big Salmon[e]	5.2 (2.9, 7.8)	8.1 (6.2, 10.0)	4.7 (3.1, 6.4)
	Teslin[e]	9.9 (5.9, 14.4)	10.4 (8.4, 12.5)	9.2 (7.0, 11.7)
	Headwaters[e]	1.5 (0.6, 2.8)	1.6 (0.8, 2.5)	2.3 (1.2, 3.6)

[a]Nonterminal main-stem reaches, including small tributaries associated with the main river.
[b]Combined tributaries in the upper reaches of the drainage.
[c]From Rapids to the Yukon–Porcupine River confluence.
[d]Upriver from the Yukon–Porcupine River confluence.
[e]Canadian reaches of the basin.