Investigation of Migratory Timing and Rates of Chinook Salmon Bound for the Kwethluk and Kisaralik Rivers Using Radio Telemetry

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Abstract

Detailed information regarding migratory behavior (i.e., phenology and rate of travel) of specific Pacific salmon *Oncorhynchus* spp. substocks can be used to design management strategies focused on protecting substocks from harvest when desired, however, this information is often lacking. The Kwethluk and Kisaralik Rivers are two tributaries of the lower Kuskokwim River that originate and flow through the Yukon Delta National Wildlife Refuge in western Alaska. Although these two systems are the primary Chinook Salmon-producing tributaries within the Yukon Delta National Wildlife Refuge, little is known about migratory behavior of Chinook Salmon destined for these rivers. In 2015 and 2016, 119 Chinook Salmon tagged with radio telemetry transmitters entered either the Kwethluk or Kisaralik Rivers and were tracked throughout their migration to their assumed final spawning location using both ground- and aerial-based tracking methods. We compared migration timing and swim speeds between fish bound for these two rivers and between fish of different sizes and compared the consistency among the two years. In general, we found that fish bound for the Kwethluk and Kisaralik Rivers exhibited similar migration behaviors in 2015 and 2016, including entry timing into the Kuskokwim River and migration rates once in the tributaries. A key finding was that Chinook Salmon swam fastest (range of means between years: 20-45 km/d) in the main-stem Kuskokwim River and slowed significantly (4-15 km/d) upon entry into lower portions of the tributaries. Our findings have relevance for harvest management strategies, for example temporal fishery closures will impact Chinook Salmon bound for both the Kwethluk and Kisaralik River equally given their broad overlap in entry timing, and that individuals will remain vulnerable to harvest for longer periods when located in tributaries rather than the portion of the main-stem directly below the tributary confluences.
Key words: Chinook Salmon, Telemetry, Migration

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Introduction

Chinook Salmon *Oncorhynchus tshawytscha* spawn in rivers throughout the northern Pacific Rim (Heard et al. 2007) and have among the most complex life history strategies of all the anadromous Pacific salmon, showing a wide (3-8 year) range in age-at-maturity and often display fine-scale differences in adult migration timing (Smith and Liller 2017a; Eiler et al. 2014). The abundance of the Kuskokwim River Chinook Salmon population, located in western Alaska, has oscillated for the past four decades (1976–2018 mean: 215,000 fish; range: 79,000–403,000 fish) with recent run sizes well below the long-term average (2010–2017 mean: 111,000 fish; Smith 2019). Kuskokwim River Chinook Salmon are particularly valued by local subsistence users and have accounted for approximately 42% (range: 15%–52%) of subsistence salmon harvests in the Kuskokwim River between 1990 and 2009 (Hamazaki 2011). As much as half of the total Chinook Salmon subsistence harvest in the state of Alaska occurs in the Kuskokwim drainage (Fall et al. 2013). However, recent low run sizes have led to severe restrictions on subsistence harvests to allow drainage-wide escapement goals to be met (Poetter and Tiernan 2017). To inform decisions about the severity of restrictions, basic information on the spawning distribution, run timing, and migration rates is fundamental to understanding and managing Chinook Salmon runs and to facilitate conservation efforts when needed.

Different approaches have been used to assess the status of Chinook Salmon returns in the Kuskokwim River, including in-river test fisheries, weirs to enumerate tributary-level escapement, sonar counts, escapement indices via aerial surveys, and radio telemetry (Head and Smith 2018; Brodersen et al. 2016; Lipka and Poetter 2016; Schaberg et al. 2012). As informative as all these sources are when taken in aggregate, only radio telemetry provides information about migration rates (i.e., swim speeds) through particular sections of rivers, stock-
group-specific run timing, and the final location of fish tagged earlier in the season. River entry
timing, swim speed, and spawning location information can be important for managers deciding
when to open and close a fishery. For example, if a manager knows that a stock-group migrates
though the primary fishery area early (e.g., during the first two weeks of June), they can use time
and area closures to avoid harvesting that stock-group if desired.

From 2000–2007, the Alaska Department of Fish and Game (ADF&G) conducted radio
telemetry of Chinook Salmon destined for the middle and upper Kuskokwim River tributaries
(Stuby 2007). The Alaska Department of Fish and Game tagged Chinook Salmon captured with
drift gillnets and fish wheels and tracked them to their presumed natal tributaries using stationary
and aerial receivers (Schaberg et al. 2012). A subset of these years were used to obtain drainage-
wide estimates of total annual run abundance via the Lincoln-Peterson mark-recapture estimator
(Schaberg et al. 2012). In 2015, ADF&G started a new Chinook Salmon radio telemetry project
with a tagging location farther downriver near the village of Napakiak (Smith and Liller 2017a,
b). Like the 2007–2007 studies, the main objective of this new radio telemetry was to estimate
the drainage-wide estimates of total abundance. A benefit of moving the tagging site to the lower
Kuskokwim River was that Chinook Salmon migrations could be monitored to lower
Kuskokwim River tributaries (i.e., the Kwethluk, Kisaralik, and Tuluksak Rivers) as well as on
the main-stem within the Yukon Delta National Wildlife Refuge (YDNWR), which was not
possible in earlier telemetry projects.

In this article, we present findings about the migratory behaviors (i.e., run timing and
swim speeds) of Chinook Salmon in 2015 and 2016 bound for the Kwethluk and Kisaralik
Rivers. These two rivers are the two primary spawning systems within the YDNWR but have not
been studied as intensively as sub-populations spawning in other Kuskokwim River tributaries
with respect to Chinook Salmon migratory behavior. The objectives of this study were to: (1) investigate if there are differences between main-stem entry timing of Chinook Salmon bound for the Kwethluk and Kisaralik Rivers; (2) quantify residence time in various sections of the lower Kuskokwim River and investigate if this covaries with entry timing; (3) quantify the average swim speeds in various reaches of the lower Kuskokwim River; (4) quantify differences in final travel distances between early and late running Chinook Salmon; and (5) investigate relationships between Chinook Salmon swim speed and body size.

Considering the close proximity of the Kwethluk and Kisaralik Rivers, we expect that fish migrating to them should show similarities in behavior, as was found by Eiler et al. (2014) for sub-populations with close proximity in Yukon River Chinook Salmon. We expect migration rates to be consistent with those reported by Eiler et al. (2014) as well, given the similarities between the Yukon and Kuskokwim Rivers (non-impounded large river basins located in western Alaska). Further, we expect that later-running fish will spend less time in the main-stem Kuskokwim River than their earlier-running counterparts, as reported by Clark et al. (2015) for Chinook Salmon migrating to the Togiak River in southwestern Alaska.

Methods

Study Area

The study area encompassed the lower and tidally influenced portion of the main-stem Kuskokwim River as well as the Kwethluk and Kisaralik Rivers, which are tributaries to the Kuskokwim River (longitude: 162°W–159.5°W; latitude: 60°N–61°N; approximate; Figure 1). The Kwethluk and Kisaralik Rivers originate in the Kuskokwim Mountains of southwest Alaska, then flow through the YDNWR en route to the Kuskokwim River and finally the Bering Sea. These two rivers are the two predominate salmon-producing Chinook Salmon tributaries in the
YDNWR and support four species of anadromous Pacific salmon in addition to Chinook Salmon: Chum Salmon *O. keta*, Sockeye Salmon *O. nerka*, Pink Salmon *O. gorbuscha*, and Coho Salmon *O. kisutch*. The area from the village of Kwethluk downstream to the mouth of the Kuskokwim (the main-stem portion of the study area, Figure 1) is one of Alaska’s most intensive subsistence fisheries, accounting for the majority (70%) of Chinook Salmon harvest in the Kuskokwim River (U.S. Fish and Wildlife Service 1988; Burkey et al. 2001; Shelden et al. 2016; Staton and Coggins 2016).

**Capture and Tracking**

Capture and tagging of Chinook Salmon occurred downriver from the confluence of the Johnson and Kuskokwim Rivers (river kilometer [rkm] 84; Figure 1). Drift gillnets were used to capture medium to large size adult Chinook Salmon (>450 mm mid-eye to tail fork length [METF]). Gillnets had a stretched mesh size of 19.1 cm (7.5 in), were 45 meshes deep (8.6 m), and were constructed of multi-fiber monofilament (MT83 twine and shade 66 Green) with a D/K knot type. Size 11 closed cell foam floats were used with a 1.1 cm cork line. The lead line was size 95 and the mesh was hung at a 2:1 ratio for a finished length of 45.7 m (25 fathoms).

To minimize fish stress, gillnets were retrieved immediately after a fish became entangled. Captured Chinook Salmon were removed from the net, placed in a tote containing fresh river water, and immobilized in a soft mesh cradle. Fish were measured to the nearest mm METF, and sex was assigned based on visual inspection of secondary sexual characteristics. However, upon further inspection of recaptured fish later in the spawning migration when secondary sex characteristics were substantially more pronounced (at weirs located within spawning tributaries), Smith and Liller (2017a) reported that sex assignment at the tag site had an error rate of 24%, rendering this assignment unreliable. Thus, recorded sex of tagged fish was
not included in our analyses. A physical examination was performed on all captured Chinook Salmon; the examination ranked fish on a scale of 1–4, with 1 being good condition with no injuries, 2 having minor injuries, 3 having major injuries, and 4 being deceased. Only fish that received a rank of 1 or 2 were tagged.

Chinook Salmon that passed the physical examination were fitted with a uniquely coded esophageal radio tag (Advanced Telemetry Systems, Inc.). A total of 623 and 621 Chinook Salmon were fitted with radio transmitters in 2015 and 2016, respectively. Two sizes of radio transmitters were used to ensure transmitters did not exceed 2% of the fish’s body weight (Cooke et al. 2013). Model F1840B tags (20 g total weight) were used for fish with a METF length between 450 mm and 550 mm, while larger model F1845B tags (24 g total weight) were used for fish greater than 550 mm. Any captured Chinook Salmon smaller than 450 mm were not tagged. Battery life was 180 days for both sizes of radio tags. Insertion of radio transmitters followed methods outlined by Stuby (2007) and Chinook Salmon were released immediately following tagging under their own power. Radio transmitters were deployed in proportion to run abundance based on a schedule developed from historical run timings observed at the Bethel test fishery (BTF) located 39 rkm upriver from the tag site. The deployment schedule was modified in-season using within-year run timing information from the BTF to mimic actual run timing observed.

Four stationary tracking towers were used to monitor the migration of Chinook Salmon throughout the lower portion of the Kuskokwim River drainage: main-stem tower 1 (T1; rkm 130), main-stem tower 2 (T2; rkm 142), lower Kwethluk tower (LKT; rkm 157), and the Kwethluk weir tower (KWT; rkm 235; Figure 1; Table 1). No towers were placed in the Kisaralik River. Stationary towers were equipped with an ATS model 4500 receiver that had an
The receiver, 2 deep-cycle 12V batteries, and associated components were securely housed in a lockable weather resistant steel box. Two 4-element Yagi antennas were mounted on a mast elevated 2–10 m above the ground. The tower was powered by a 95W solar panel. Each receiver was programmed to receive from both antennas simultaneously and scan through the list of tag frequencies at 3 s intervals. When a signal of sufficient strength was detected, the receiver paused for up to 12 s on each antenna to decode and record tag information. The relatively short cycle period minimized the chance of radio-tagged fish passing the receiver site without being detected. Each stationary telemetry station was tested at assembly to confirm that detections would be recorded across the entire river channel width. In addition, a reference tag was affixed downriver of the tower to confirm operational status of the receiver.

In addition to stationary tracking, aerial telemetry tracking flights were performed annually between June 1 and August 9 to monitor upriver movement and determine final location. Tracking surveys were conducted with a fixed wing aircraft, pilot, and surveyor(s) who operated a R4500 data logger(s). Scan time for each frequency was 2 s. A single H-antenna was mounted on each wing strut. Prior to all surveys, equipment operation status was checked by flying over a known reference tag. Surveys were flown at approximately 120 km/h at an altitude between 100 m and 300 m above the center of the main river channel. The surveyor prompted the data logger to record georeferenced tag information once a radio transmitter was detected. A detailed review of tracking methods can be found in Smith and Liller (2017a, b), but surveys were generally flown to ensure all portions of the study area were passed once while recording such that all areas received similar tracking effort.

Data Preparation and Analysis
Our dataset (provided in an online supplement; Data S1) included individual fish detections made by (1) tagging (first detection), (2) stationary telemetry towers, and (3) mobile aerial tracking. The raw variables for each detection were an individual identifier (ID), date and time of day (to the nearest minute) of the detection, and latitude and longitude of the receiver when the detection with the highest signal strength was found. Prior to analysis, tracking data were reviewed among all aerial and ground-based tracking events to confirm that all tagged fish used in this study traveled to the Kisaralik and Kwethluk Rivers. Fish that did not have a clear tracking history (i.e., false detections) to these rivers were not used in the analysis. Date and time were converted into a single numeric variable, decimal day ($D$), by converting the calendar date to day-of-the year (DOY) and adding the fraction of day the detection was made. For example, a detection made at noon on June 15, 2016 would be $D = 167.5$. After the final location of each fish was determined, a stock grouping was assigned (i.e., Kwethluk or Kisaralik). The $D$ associated with tagging ($D_{tag}$) was used as a surrogate of main-stem river entry timing, which assumed that all fish swam at the same rate between the river mouth and the tag site.

The distance in rkm from the river mouth for individual $i$ at detection occasion $j$ ($RKM_{i,j}$) was determined to allow calculation of travel distances and swim speeds. A set of “keys” that indicated which latitude/longitude coordinates correspond to each of the possible discrete rkm sites at which a fish could have been detected was developed to assign $RKM_{i,j}$ (created by K. Milton, USFWS). These keys were constructed by drawing 1 km long perpendicular lines at 1 km intervals along the main-stem Kuskokwim River, the Kwethluk River, and the Kisaralik River and obtaining the coordinates of the endpoints of these perpendicular lines. The endpoints from two consecutive lines form a grid, and each detection was assigned to one of these grids (and as a result, a $RKM_{i,j}$).
Swim speed \((v)\) was defined as the distance traveled divided by the time elapsed between two consecutive detections for any given fish:

\[
v_{i,j} = \frac{RKM_{i,j} - RKM_{i,j-1}}{D_{i,j} - D_{i,j-1}}
\]  

(1)

where \(D_{i,j}\) is the decimal day of detection \(j\) on individual \(i\). To remove any potential biases resulting from a “tagging effect” (fish swimming slowly immediately after tagging during recovery; Smith and Liller 2017a; Eiler et al. 2014), we discarded any detections downstream of \(T1\) in calculations of swim speed (\(T1\) was approximately 45 rkm upstream of the tagging site). Note that if an individual was detected downstream of a previous detection, \(v\) for that pair would be negative. As such, the variable \(v\) can more appropriately be viewed as a net upstream progress over a given time interval.

**Entry Timing**

Differences in entry timing between Kwethluk- and Kisaralik-bound fish (Objective 1) were assessed using two methods: year specific \(t\)-tests on \(D_{tag}\) between stock-groups (Table 2; Model 1) and logistic regression. For the logistic regression, the response variable was a binary indicator for each fish, coded as a 1 if the fish was ultimately bound for the Kwethluk River and a 0 if the fish was bound for the Kisaralik River, and \(D_{tag}\) was used as the independent variable (Table 2; Model 2). This logistic regression provided as output a daily probability that a tagged fish bound for either of these two rivers would be bound for the Kwethluk River; if this probability changed substantially over the duration of the study that would provide evidence for different run timing between fish bound for the Kwethluk and Kisaralik Rivers.

**Residence Time**

Residence time in various areas of the lower Kuskokwim River (Objective 2) was assessed using the number of days elapsed between two stationary tower detections. This
variable was treated as the response variable in a set of regressions where $D_{tag}$ was the predictor variable to determine if residence time was related to entry timing (Table 2; Models 3–8). Residence times were also compared between years using independent $t$-tests to gauge consistency in residence time between years.

**Spatial Patterns in Swim Speed**

Spatial patterns in swim speed (Objective 3) were analyzed using a combination of tower and aerial survey detections to compare $v_s$ where $s$ is a stratum identifier (KUSKO-1, KUSKO-2, KWE-1, etc.; Figure 1). Two consecutive detections where used to obtain $v_{i,j}$ as in Eq. 1, then each detection $j$ of each fish $i$ was assigned to the appropriate stratum $s$ according the midpoint of $RKM_{i,j}$ and $RKM_{i,j-1}$. Multiple observations of the same fish with a strata were averaged to obtain $v_{i,s}$. Given that multiple observations of the same fish were made between strata, these observations were likely not all independent. This was accounted for by using a linear mixed effects model (LMM) with $v_{i,s}$ as the response variable, stratum as a categorical predictor variable, and random intercepts for each individual to allow for the possibility of some individual fish swimming faster/slower than others between strata. The LMM was fitted to each year separately using the R package `nlme` (Pinheiro et al. 2016). Multiple comparisons of the mean $v_s$ between all strata $s$ within a year were conducted using a Tukey-Kramer post-hoc adjustment to maintain the experiment-wise error rate at $\alpha = 0.05$ using the R package `lsmeans` (Lenth 2016).

**Travel Distance vs. Entry Timing**

Simple linear regression was used with the $RKM_{i,j}$ on the last flight of the year as the response variable and $D_{tag}$ as the predictor variable to assess if fish that entered earlier in the season were destined to travel farther up a spawning tributary (Objective 4; Table 2; Model 9). The final aerial telemetry flight of the year was conducted on August 8 and August 9 in 2015 and...
263 2016, respectively. Aerial telemetry flights in both years had the same spatial coverage and followed similar tracking routes.

265 *Swim Speed vs. Fish Size*

 Associations between swim speed and fish size (Objective 5) were evaluated using only the area between T1 and KWT, as this was the longest stretch of river with many observed travel durations. Speed for each fish $v_i$ was obtained using Eq. 1 where $D_{i,j}$ and $D_{i,j-1}$ were set at the $D$ of the KWT and T1 detections for fish $i$, respectively and $RK_{M_{i,j}}$ and $RK_{M_{i,j-1}}$ set equal to those of the KWT and T1 locations, respectively (thus excluding Kisaralik-bound fish from this analysis). Values of $v_i$ were treated as the response variable and fish length was treated as the predictor variable in simple linear regression models fitted to each year separately.

 Model assumptions (e.g., normality of residuals, lack of residual patterns, etc.) for all fitted models were checked visually but not using formal tests. For tests of statistical significance, $\alpha = 0.05$ was used in all cases and all presented confidence limits are at the 95% level. Except where otherwise noted, the same models were fitted to each year separately. All data manipulation and analyses were conducted in the statistical program R (R Core Team 2015).

**Results**

 A total of 52 and 67 radio-tagged fish were tracked to the Kwethluk and Kisaralik Rivers in 2015 and 2016, respectively, and made up approximately 10% of all tagged Chinook Salmon that returned to the Kuskokwim River these years. Kwethluk-bound individuals made up 71% and 73% of tagged fish spawning in the Kwethluk or Kisaralik Rivers in 2015 and 2016, respectively. A total of 544 and 521 unique fish detections were made in 2015 and 2016, respectively (excluding tagging). Of these detections, 70% in 2015 and 60% in 2016 resulted
solely from aerial flights which, unlike the towers, had the ability to detect the same individual at multiple times during its migration.

**Entry Timing**

There was no indication that Kisaralik and Kwethluk-bound individuals had different entry timing into the Kuskokwim River based on $D_{tag}$ in either 2015 or 2016. This was supported by both the $t$-tests (Table 2; Model 1) and the logistic regressions (Table 2; Model 2). The general flatness and broad level of uncertainty of the fitted logistic regression lines indicate that that Kwethluk and Kisaralik-bound fish migrate through the lower Kuskokwim River mixed together (Figure 2).

**Residence Time**

In 2015, there was no evidence that fish tagged later in the season spent more time in any of the defined river sections than fish tagged earlier (Table 2; Models 3–8; small effects and wide confidence limits). However, in 2016, the regressions of T1–LKT, T1–KWT, T2–KWT and LKT–KWT had significant (and negative) entry timing effects. The negative effect indicates that the time spent within a river section declined as the season progressed, showing that fish swam faster the later they entered the Kuskokwim River.

In comparing the average residence time between years, we found that residence time was generally longer in 2015 than in 2016. However, significant differences were only found for the longest sections with Kwethluk weir as the upper endpoint (T1 – KWT, T2 – KWT, and LKT – KWT). Residence times in shorter river sections and those that did not involve a tributary were not significant, indicating that the differences in residence time between these years was a result of differences in migration rate once in the Kwethluk River.

**Spatial Patterns in Swim Speed**
The LMM identified clear differences in migration rates among river sections that were consistent between years (Figure 3), namely that fish slowed as their migration progressed. Fish swam fastest in the first main-stem strata (KUSKO-1; mean 40 and 30 rkm/d in 2015 and 2016, respectively), slowed upon reaching KUSKO-2 (mean of approximately 20 rkm/d in both years, and slowed even more to average speeds of approximately 10 rkm/d in the lower sections of the tributaries (KWE-1 and KIS-1). The mean speed in the upper portions of the tributaries (KWE-2 and KIS-2) was lower than the downstream portions in both years, though the only significant comparison of these was the 2016 KWE-1 vs. KWE-2 comparison.

**Travel Distance vs. Entry Timing**

There was weak evidence to suggest that early-timed fish migrated further to get to a spawning location than later running fish (Table 2; Model 9). This conclusion is supported by the negative slopes in the fitted regression models (Figure 4). However, only the 2015 slope was significant and the effect was fairly minimal: fish tagged one day later than their counterparts the previous day would be expected to travel the same distance minus 0.82 rkm.

**Swim Speed vs. Fish Size**

There was no evidence to suggest that fish of different sizes migrated at different rates between T1 and KWT (Table 2; Model 10). The slope coefficients for both 2015 and 2016 were not significantly different from zero. Furthermore, both years had small effect sizes: -0.01 (2016) and 0.01 (2016) rkm per day for every one mm increase in fish length.

**Discussion**

In order to draw meaningful conclusions from the results in this study, we must make the assumption that untagged (unobserved) fish were harvested at the same rate and also behaved similarly with regards to swim speed, river entry, residency time, and final tributary location as
the tagged fish for which we have observations (Rogers and White 2007). Making claims about
the ~100 tagged fish in this study is of little utility alone, rather we are much more interested in
how the larger population of fish behaves, but we cannot draw inferences about those fish
without the assumption of representativeness. The Alaska Department of Fish and Game exerted
extensive efforts to ensure that all run components were tagged in proportion to their abundance
and that the tagging process was as minimally-intrusive as possible (Rogers and White 2007;
Smith and Liller 2017a, b). Smith and Liller (2017 a, b) confirmed that radio tags were deployed
in proportion to abundance and the harvest rates of tagged (2015–12%; 2016–17%) and
untagged fish (2015–13%; 2016–24%) were similar for both study years (Smith 2019). Thus, we
demn this assumption (i.e., that the sampled fish were representative of the larger population) to
be reasonably valid.

No differences were detected in run timing between fish bound for the Kisaralik and
Kwethluk Rivers in 2015 and 2016. Fish bound for the Kisaralik and Kwethluk Rivers appeared
to enter the Kuskokwim River main-stem throughout the month of June. Knowledge of the entry
run timing of Kisaralik and Kwethluk River Chinook Salmon should be used to when developing
management actions to regulate main-stem Kuskokwim River harvest of fish returning to these
two lower Kuskokwim River tributaries. Given the similar run entry timings, any management
action aimed at protecting escapement to one population can be assumed to equally protect the
other population. Further, management actions that close the main-stem fishery for a blocked
time period (i.e., 3–10 days) to promote escapement of Kwethluk and Kisaralik River Chinook
Salmon will not likely have the same management effects that have been observed from other
Kuskokwim river Chinook Salmon stock-groups. For example, Kuskokwim River headwater
Chinook Salmon stock-groups tend to enter the Kuskokwim River earliest in the season and have
a more compressed entry timing distribution compared to Kwethluk and Kisaralik River fish 
(Smith and Liller 2017a, b). Early season main-stem fishery closures from 2014–2016 have 
resulted in record-sized escapements for headwater stock-groups (Smith 2019). Given the run 
timing of Kisaralik and Kwethluk River Chinook Salmon, these early season closures have 
provided protection to early run Kisaralik and Kwethluk River Chinook salmon; however, 
additional management actions would be required to protect the middle and later run fish. 
Toward this end, management actions could include block-style closures of the main-stem lower 
river fishery downriver from these tributaries during all temporal components of the run. The 
duration of closures would need to be commensurate with the level of conservation concern. 

Our results indicate that Kwethluk-bound fish could travel from T1, which is at the 
spatial core of the lower river salmon fishery (Staton and Coggins 2016), to sanctuary from 
harvest in the lower portion the Kwethluk River (LKT) in 1–3 days if spawning tributaries 
continue to be closed to fishing as they have in recent years. However, this study only looked at 
Kisaralik and Kwethluk Chinook Salmon; fish traveling to the many tributaries in the middle- 
and upper-Kuskokwim drainage remain in the main-stem (thus vulnerable to harvest) for a 
longer period. Smith and Liller (2017a, b) studied migration rates of fish destined for spawning 
in these more distant areas within the Kuskokwim and found that fish swim approximately 35 
rkm/d in this and other portions of the main-stem Kuskokwim River, with no systematic 
variation explained by tributary-group (i.e., spawning spatial area). This knowledge of swim 
speed through the Kuskokwim River is very useful to managers. For example, these data can be 
used to estimate how long it might take river reach to fill with fish again following a fishing 
opportunity with high exploitation, or how long it will likely take a pulse of fish to clear the 
highest-effort areas in times of conservation.
In 2016, we observed that fish tagged in the early part of the season had longer residence times than fish tagged later in the season, but this was not true of 2015. This result may be part of Chinook Salmon biology (Quinn 2005), interannual differences in environmental conditions (Keefer et al. 2004; Neuneker 2017; Strange 2012), or simply a result of handling effects (e.g., it is possible that the tagging crew became more efficient as the season progressed and the tagging process became less stressful on fish, resulting in faster swim speeds later in the season; Bernard et al. 1999). Because the pattern was observed in 2016 but not in 2015, we believe that the 2016 result (shorter residence time for later running fish) is not a general conclusion. Limited environmental data are available for the Kuskokwim River to elucidate residence time differences due to environmental factors; however, water temperature data at the BTF indicates that both years had similar temperatures with mean temperatures for 2015 and 2016 being 15.0°C (range: 10.0–20.0°C) and 14.8°C (range: 12.0–18.0°C), respectively. The primary reason we were interested in the time-of-season effect is related to the vulnerability concept: if early-running fish take more time to migrate into tributaries they would remain vulnerable to the fishery for a longer period of time. Given local subsistence fishers have historically tended to fish more during the early portion of the Chinook Salmon run (Hamazaki 2008) and the study area encompasses the spatial core of the lower river salmon fishery (Staton and Coggins 2016), longer residence times early in the season could further increase the relative exploitation rate on Chinook Salmon during the earlier periods of the fishery. However, given the lack of agreement between 2015 and 2016, additional research is needed to identify what factors (e.g., biological or environmental) explain residency time.

There was weak evidence to suggest that earlier-running fish traveled further up the tributaries. Based on studies by Stuby (2007) and Smith and Liller (2017a), we know that
Chinook Salmon bound for the headwater tributaries enter the Kuskokwim River earlier than fish bound for the middle river tributaries: the difference in the median date of tag deployment has varied between three and 10 days. Migration distance was also an important covariate explaining variation in migration timing found in the study by Clark et al. (2015) on Togiak River Chinook Salmon, and by Neuneker (2017) on the Stikine and Taku Rivers. Both studies identified that early-run fish generally traveled the farthest to spawning locations. These previous studies focused on drainage-wide spatial scale. Our study was focused on the smaller tributary scale and we, therefore, found it interesting that a similar result arose (i.e., early fish traveled farthest) at the tributary scale investigated in this study (Figure 1).

An important assumption of our analysis regarding total travel distance was that the last aerial telemetry flight locations were the final destinations of all Chinook Salmon. It is possible that some later-run fish were still en route to their final destination on the date of the last telemetry flights. Alternatively, some early-run fish may have spawned, and subsequently drifted down river (Murdoch et al. 2010). Peak spawning ground abundance of Kuskokwim River Chinook Salmon occurs between late July and early August (Molyneaux and Brannian 2006). Therefore, while some fish many have been still en route to spawning grounds and other fish may have drifted down stream after spawning, the effect on data analysis and interpretation is assumed to be minimal based on the last telemetry flight survey date. Future telemetry flights should be conducted later into August to gain a better understanding of final destinations for tagged fish.

When considering our swim speed results, it is important to place them in the context of other investigations of swim speeds in large river basins. One study in particular stands out as a good candidate for comparison: Eiler et al.’s (2014) investigation of Chinook Salmon migratory
patterns in the Yukon River. The Kuskokwim and Yukon River Chinook Salmon share many common characteristics (e.g., recent common ancestor and morphologically similar) and being spatially close in proximity, these drainages share many common environmental and geomorphic characteristics. The Yukon River study was a much broader-scale investigation of movement patterns between distinct stocks than that presented in our study, although some interesting similarities were apparent. First, Eiler et al. (2014) found that stocks bound for the same region exhibited similar swim speeds. The Kisaralik and Kwethluk Rivers can certainly be considered in the same region when considering the much larger Kuskokwim drainage, and our findings suggest Chinook Salmon migrating to these two rivers have similar swim speeds. Second, the swim speeds within the main-stem Kuskokwim River from our study (20–45 km/d within KUSKO-1 and KUSKO-2) were within the range of speeds found for the Yukon River (25–65 km/d). Third, the Chinook Salmon studied in Eiler et al. (2014) showed a large amount of individual variation. Individuals typically showed consistent behaviors with slow or fast fish in one area likely to also be slow or fast fish, respectively, elsewhere. We certainly saw high amounts of variation among individuals, but we did not specifically characterize fish as slow or fast, as was done by Eiler et al. (2014).

The findings of this study showed important themes that are potentially useful for management discussions and decisions. Broadly speaking, we found (1) spatial patterns in swim speeds, (2) no differences in migratory behavior based on fish size, and (3) consistent migration characters between fish bound for the Kwethluk and the Kisaralik Rivers. As an example management use, the finding that fish swam faster in the shorter length main-stem Kuskokwim River reaches than in the longer length tributaries could be used to justify tributary closures as fish may remain vulnerable to gear set in the tributaries for a longer period of time than in the
main-stem. Additionally, the quantification of the amount of time spent in the main-stem spatial strata we used could be used to inform how long the fishery should remain closed to allow a pulse of fish to pass through.

Acknowledgements

We would like to thank Alaska Department of Fish and Game personnel for their efforts in deploying telemetry tags and U.S. Fish and Wildlife Service pilot R. Sundown for his many hours spent tracking fish within the Yukon Delta National Wildlife Refuge. We thank L. Coggins, K. Harper, Z. Liller, B. McCaffery, K. Stahlnecker, G. Decossas, M. Catalano, and two anonymous reviewers for providing helpful comments on earlier drafts of this article. We would like to thank L. Horne (Auburn University) for producing Figure 1 and K. Milton (U.S. Fish and Wildlife Service) for producing the spatial keys allowing assignment of specific river kilometers to each detection. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.
Supplemental Material

http://www.adfg.alaska.gov/FedAidPDFs/RIR.3A.2016.06.pdf (1,217 KB PDF)

http://www.adfg.alaska.gov/FedAidPDFs/RIR.3A.2001.34.pdf (37,661 KB PDF)


http://www.adfg.alaska.gov/FedAidPDFs/FMS11-09.pdf (23,961 KB PDF)


http://www.adfg.alaska.gov/FedAidPDFs/FDS16-07.pdf (1,592 KB PDF)


Data S1. A data file in text file format containing individual fish detections made by receivers at tower locations or fixed-wing aircraft. Variables included are: ID (fish identifier), year (year of detection), date (date of detection), time (time of detection), decimal day (the day of the year plus the fraction of a day completed prior to detection), type (aerial vs. specific towers), latitude and longitude of the receiver at the time of detection, river kilometer (distance from the Kuskokwim River mouth), and the river in which the detection was made (Kuskokwim River main-stem vs. one of the tributaries).
REFERENCES


Lipka, C., and A. Poetter. 2016. Characterization of the 2014 salmon runs in the Kuskokwim River based on the test fishery at Bethel. Alaska Department of Fish and Game, Fishery Data Series No. 16-07, Anchorage.


**TABLE CAPTIONS**

**Table 1.** Coordinates of the tagging site and stationary tracking towers, expressed in decimal degrees, that were used to assess the movements of radio-tagged Kuskokwim River Chinook Salmon *Oncorhynchus tshawytscha* migrating to the Kwethluk and Kisaralik Rivers in western Alaska in 2015 and 2016.

**Table 2.** Summary of fitted models, excluding *t*-tests, that were used to compare the migratory behavior of radio-tagged Kuskokwim River Chinook Salmon *Oncorhynchus tshawytscha* migrating to the Kwethluk and Kisaralik Rivers in western Alaska in 2015 and 2016. “Obj #” references the specific objective the model pertains to, as described in the text. Bold values denote cases in which $\beta_1$ was significantly different than zero. Values in parentheses are 95% confidence limits.

**Table 3.** Mean residence time of radio-tagged Kwethluk and Kisaralik River migrating Chinook Salmon *Oncorhynchus tshawytscha* between two (not necessarily consecutive) stationary telemetry towers positioned in the lower Kuskokwim River in western Alaska in 2015 and 2016. The column labeled “RKM” represents the distance between stationary tower locations, in river kilometers. Bold values denote significant differences between years (obtained via independent two-tailed *t*-tests). Values in parentheses are 95% confidence limits.
Table 1.

<table>
<thead>
<tr>
<th>Point of Interest</th>
<th>Latitude</th>
<th>Longitude</th>
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<tbody>
<tr>
<td>Tag Site</td>
<td>60.64</td>
<td>-162.09</td>
</tr>
<tr>
<td>Main Stem Tower 1 (T1)</td>
<td>60.84</td>
<td>-161.65</td>
</tr>
<tr>
<td>Main Stem Tower 2 (T2)</td>
<td>60.80</td>
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</tr>
<tr>
<td>Lower Kwethluk Tower (LKT)</td>
<td>60.78</td>
<td>-161.39</td>
</tr>
<tr>
<td>Kwethluk Weir Tower (KWT)</td>
<td>60.52</td>
<td>-161.09</td>
</tr>
</tbody>
</table>
Table 2.

<table>
<thead>
<tr>
<th>Obj #</th>
<th>Model #</th>
<th>Linear Predictor</th>
<th>Likelihood</th>
<th>Response Variable ((y))</th>
<th>Predictor Variable ((x))</th>
<th>2015 N</th>
<th>2015 (\hat{\beta}_1)</th>
<th>2016 N</th>
<th>2016 (\hat{\beta}_1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>(\mu_i = \beta_0 + \beta_1 x_i) (y_i \sim N(\mu_i, \sigma))</td>
<td>(D_{tag})</td>
<td>Kisaralik Fish: (x_i = 0) Kwethluk Fish: (x_i = 1)</td>
<td>(D_{tag})</td>
<td>52</td>
<td>-0.82 ((-8.23, 6.59))</td>
<td>67</td>
<td>3 ((-2.57, 8.57))</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>(\text{logit}(p_d) = \beta_0 + \beta_1 x_d) (y_d \sim \text{Bin}(p_d, N_d))</td>
<td>Number of Kwethluk-bound fish tagged each day</td>
<td>(D_{tag})</td>
<td>52</td>
<td>-0.01 ((-0.06, 0.05))</td>
<td>67</td>
<td>0.03 ((-0.02, 0.09))</td>
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</tr>
<tr>
<td>2</td>
<td>3</td>
<td>(\mu_i = \beta_0 + \beta_1 x_i) (y_i \sim N(\mu_i, \sigma))</td>
<td>Days between T1 – T2 detections</td>
<td>(D_{tag})</td>
<td>42</td>
<td>0.01 ((-0.03, 0.04))</td>
<td>43</td>
<td>0.01 ((-0.03, 0.04))</td>
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<tr>
<td>2</td>
<td>4</td>
<td>(\mu_i = \beta_0 + \beta_1 x_i) (y_i \sim N(\mu_i, \sigma))</td>
<td>Days between T1 – LKT detections</td>
<td>(D_{tag})</td>
<td>27</td>
<td>-0.02 ((-0.09, 0.05))</td>
<td>34</td>
<td>-0.09 ((-0.18, -0.01))</td>
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<td>(\mu_i = \beta_0 + \beta_1 x_i) (y_i \sim N(\mu_i, \sigma))</td>
<td>Days between T1 – KWT detections</td>
<td>(D_{tag})</td>
<td>32</td>
<td>-0.04 ((-0.2, 0.13))</td>
<td>34</td>
<td>-0.19 ((-0.31, -0.06))</td>
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<td>6</td>
<td>(\mu_i = \beta_0 + \beta_1 x_i) (y_i \sim N(\mu_i, \sigma))</td>
<td>Days between T2 – LKT detections</td>
<td>(D_{tag})</td>
<td>26</td>
<td>0 ((-0.05, 0.06))</td>
<td>36</td>
<td>-0.08 ((-0.17, 0.01))</td>
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<td>7</td>
<td>(\mu_i = \beta_0 + \beta_1 x_i) (y_i \sim N(\mu_i, \sigma))</td>
<td>Days between T2 – KWT detections</td>
<td>(D_{tag})</td>
<td>33</td>
<td>-0.06 ((-0.21, 0.1))</td>
<td>36</td>
<td>-0.06 ((-0.31, -0.09))</td>
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<td>2</td>
<td>8</td>
<td>(\mu_i = \beta_0 + \beta_1 x_i) (y_i \sim N(\mu_i, \sigma))</td>
<td>Days between LKT – KWT detections</td>
<td>(D_{tag})</td>
<td>29</td>
<td>-0.05 ((-0.22, 0.13))</td>
<td>48</td>
<td>-0.13 ((-0.22, -0.04))</td>
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<tr>
<td>4</td>
<td>9</td>
<td>(\mu_i = \beta_0 + \beta_1 x_i) (y_i \sim N(\mu_i, \sigma))</td>
<td>“Final” RKM</td>
<td>(D_{tag})</td>
<td>47</td>
<td>-0.82 ((-1.63, -0.01))</td>
<td>43</td>
<td>-0.71 ((-1.97, 0.54))</td>
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<td>5</td>
<td>10</td>
<td>(\mu_i = \beta_0 + \beta_1 x_i) (y_i \sim N(\mu_i, \sigma))</td>
<td>Speed between T1 - KWT</td>
<td>Fish length</td>
<td>32</td>
<td>-0.01 ((-0.02, 0.01))</td>
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<td>0.01 ((-0.02, 0.04))</td>
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<tr>
<td>Locations (Lower – Upper)</td>
<td>rkm</td>
<td>Days Between Towers</td>
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<td></td>
<td></td>
<td>2015</td>
<td>2016</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>T1 – T2</td>
<td>12</td>
<td>0.65 (0.26,1.03)</td>
<td>0.77 (0.41,1.12)</td>
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<tr>
<td>T1 – LKT</td>
<td>27</td>
<td>1.68 (0.97,2.38)</td>
<td>2.3 (1.49,3.11)</td>
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<tr>
<td>T1 – KWT</td>
<td>105</td>
<td>15.41 (13.55,17.27)</td>
<td>9.71 (8.49,10.92)</td>
<td></td>
<td></td>
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<tr>
<td>T2 – LKT</td>
<td>15</td>
<td>1.12 (0.48,1.77)</td>
<td>1.46 (0.61,2.30)</td>
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<tr>
<td>T2 – KWT</td>
<td>93</td>
<td>14.47 (12.54,16.40)</td>
<td>8.96 (7.81-10.11)</td>
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<tr>
<td>LKT – KWT</td>
<td>78</td>
<td>13.71 (11.65-15.76)</td>
<td>7.05 (6.15-7.95)</td>
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</table>
FIGURE CAPTIONS

Figure 1. Map of the portion of the Kuskokwim River drainage, western Alaska, that served as the study area for tracking radio-tagged Chinook Salmon *Oncorhynchus tshawytscha* in 2015 and 2016 to the spawning tributaries of interest: the Kwethluk and Kisaralik Rivers. Triangles denote telemetry tower locations and the tagging site is denoted separately. “Censored data” refers to the area in which telemetry detections were not used for swim speed calculations due to recovery following tagging. Two insets are shown: (top) a map of Alaska showing where in the state the study area is located as well as the boundaries of the Yukon Delta National Wildlife Refuge (in dark grey) and (bottom) finer scale detail of the main-stem strata and tower locations. The spatial strata denoted (e.g., KUSKO-1 and KWE-2) were used to analyze the swim speed of upriver migrating Chinook Salmon.

Figure 2. Stock-specific entry timing of Kuskokwim River Chinook Salmon *Oncorhynchus tshawytscha* migrating to the Kwethluk and Kisaralik Rivers in western Alaska in 2015 and 2016. Upward facing histograms are the number of fish tagged each day bound for the Kwethluk River, downward facing histograms show the number of fish tagged each day bound for the Kisaralik River, and center panels show the fitted probability that a tagged fish on a given day was bound for the Kwethluk River. Grey regions represent the 95% confidence limits of the fitted logistic regression models.

Figure 3. Swim speed (in river kilometers per day) of radio-tagged Kuskokwim River Chinook Salmon *Oncorhynchus tshawytscha* that migrated to the Kwethluk and Kisaralik Rivers in western Alaska in 2015 and 2016. The spatial strata KUSKO-1 and KUSKO-2 are located in the main-stem Kuskokwim River, whereas the other strata were located in the tributaries of interest (KWE = Kwethluk; KIS = Kisaralik; 1 = more downstream; 2 = more upstream). Swim speed
was estimated among spatial strata using a linear mixed effects model with random intercepts for each individual fish. Different letters indicate statistical significance between strata obtained using the Tukey-Kramer procedure. Statistical comparisons were made within a year only.

**Figure 4.** Relationship between the upstream distance traveled (in river kilometers) of each radio-tagged Chinook Salmon *Oncorhynchus tshawytscha* as of the last aerial detection occasion each year and the date of tagging in the lower Kuskokwim River in western Alaska. The two study years are shown: 2015 (solid points and line) and 2016 (empty points and dashed line); fitted lines are from simple linear regression analysis.