Estimated Abundance of Adult Fall Chum Salmon in the Upper Yukon River, Alaska, 1996

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Abstract

The main objective of this study was to determine the feasibility of conducting a mark-recapture experiment to estimate the abundance of fall chum salmon on the upper Yukon River. Fish wheels were used to capture and tag 17,751 fall chum salmon to generate a Darroch population estimate of the run in the Yukon River above the Tanana River, Alaska. Between August 2 and September 24 recapture wheels, 50 km upstream of the tagging site near the village of Rampart, caught 45,232 fish, of which 1,259 were tagged. Most tagged fish were caught at the recapture site within the week they were marked. A total of 2,752 fish were released with both primary and secondary marks. At the recapture site 210 fish having secondary marks were recaptured, with no primary tag loss observed. North and south bank tagged fish randomly mixed between the marking and recapture sites. Probabilities of recapture were associated with a fish's sex and/or length during some weeks, indicating that assumptions about capture probabilities at the recapture site and/or movement to recapture strata were violated. Modeling was used to determine the potential bias from violation of these assumptions. Results from this modeling demonstrated that bias was negligible if differential recapture probabilities between the sexes were due to differential movement rather than selective sampling at the recapture site. We suggest that differential migration patterns contributed to the sex specific recapture probabilities in our study. Tagged males took less time than females to reach the recapture site, and males were more likely recaptured at the recovery site in the week they were tagged than were females. Our estimate of 654,296 ± 41,954 (95% CI) fall chum salmon was within 8% of an independent estimate of 708,812 fish compiled from escapement and harvest monitoring projects conducted in the upper Yukon River. Under the conditions of our study, Darroch's population estimator was a reasonable method for determining the abundance of fall chum salmon in the upper Yukon River.

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Introduction

In 1985 the governments of the United States and Canada signed a treaty concerning transboundary Pacific salmon *Oncorhynchus* spp. (Pacific Salmon Commission 1986). The Pacific Salmon Treaty recognized the unique nature of the Yukon River fishery and directed the Pacific Salmon Commission, in Article VIII of the treaty, to take steps to clarify the issues and establish a means to manage the fishery cooperatively and equitably (Pacific Salmon Commission 1986). In keeping with this broad directive, the governments of Canada and the United States amended the Pacific Salmon Treaty in 1995 specifically to address Yukon River issues (Pacific Salmon Commission 1995).

Reaching common ground is the overall goal of the amended Pacific Salmon Treaty as it relates to the Yukon River fisheries. Specific goals of the treaty include examining current and past management practices and assessment techniques; exploring alternate regulatory measures; investigating stock separation and monitoring studies; and evaluating salmon habitat protection needs and enhancement possibilities.

Unlike the relatively short transboundary rivers in southeast Alaska and British Columbia, the Yukon River flows about 3,000 km from its headwaters in British Columbia and Yukon Territory to its mouth in western Alaska. Nearly 2,000 km of its length lies in Alaska. Chum salmon *Oncorhynchus keta* returning to the Yukon River drainage, migrate to spawning areas in the waters of both Canada and the United States. At any one time and place along the river, chum salmon from many stocks are likely to be present.

Chum salmon enter the Yukon River in two major groupings referred to as the summer and fall runs (Bergstrom et al. 1995). The two runs are genetically distinct (Wilmot et al. 1992) and differ in run timing, spawning locations, and morphology. As their names imply, summer chum salmon enter the river earlier than fall chum salmon. For in-season management purposes chum salmon entering the river before July 15 are considered summer chum salmon and those entering the river after July 15 are considered fall chum salmon, although some overlap undoubtedly occurs. Most summer chum salmon spawn in tributary streams in the lower 800 km of the Yukon River and in the Tanana River system. A smaller number spawn in the upper Yukon River in Alaska and occasionally a few enter Canadian waters (Bergstrom et al. 1995, see their Appendix D2). Summer chum salmon are not targeted by the Canadian fishery. Fall chum salmon tend to be larger than summer chum salmon and migrate to major spawning areas in the Tanana, Chandalar, and Porcupine rivers in Alaska and the upper Yukon River in Canada. Fall chum salmon are targeted by commercial and food fisheries in Alaska and the Yukon Territory, and account for most of the annual Canadian catch of Yukon River salmon (Bergstrom et al. 1995).

Escapements of fall chum salmon in the upper Yukon River are currently monitored on the Chandalar and Sheenjek rivers in Alaska and on the Fishing Branch River and the Yukon River mainstem in Canada. These monitoring sites are believed to account for a large portion of the upper Yukon River fall chum salmon escapement, but the actual total escapement is unknown.

A study was proposed by the U. S. Fish and Wildlife Service, and endorsed by the Yukon River Joint Technical Committee (JTC) of the Pacific Salmon Commission, to determine the feasibility of conducting a mark-recapture experiment to provide weekly and total abundance estimates of adult fall chum salmon in the mainstem of the upper Yukon River. Agreement between mark-recapture experiment estimates, and harvest and escapement estimates from the four monitoring sites on the upper Yukon River, would provide assurance that most of the fall chum salmon run is being monitored. This report documents the results of this feasibility study.

Study Area

The Yukon River is the fifth largest drainage in North America draining an area of approximately 855,000 km^2 (Bergstrom et al. 1995). Three of the tributaries that join the Yukon River are major rivers themselves; each is approximately 1,000 km in length. They are the Koyukuk, Tanana and Porcupine rivers, joining the Yukon River at 800, 1,100 and 1,600 km from its mouth.

The upper Yukon River, upstream from the Tanana River, is almost 2 km at it widest point and flows from 6 to 12 km per hour. Due to the glacial origins of some of its tributaries, the Yukon River is very silty during the summer, but it clears during winter. The region experiences a continental climate with long cold winters and brief warm summers. Air temperatures below freezing are common during September. The river generally freezes by late October or November and the ice remains until May of the following year.

Two study sites were maintained on the mainstem Yukon River upstream from the Tanana River confluence (Figure 1). The location was selected to minimize the capture of fall chum salmon returning to the Tanana River drainage, the only major area of fall chum salmon spawning downstream from the study area. The marking site was located at an area known locally as “The Rapids,” a narrow canyon 1,176 km from the mouth of the Yukon River. The recapture site was 50 km upstream from the marking site, near the village of Rampart.

Methods

The study was designed to estimate a temporally stratified population using a two-event mark-recapture experiment. Darroch’s (1961) model was used to generate weekly and total estimates of fall chum salmon in the upper Yukon River. In using Darroch’s model we made five explicit assumptions:

1) Closure - all fish must have a non-zero probability of capture in one of the marking strata and all fish in the recapture stratum must have been present in at least one marking stratum;

2) No tag loss - fish must retain their mark and be correctly identified;

3) All fish in a given recapture stratum, marked and unmarked, have equal probability of capture;

4) All fish, marked and unmarked, in a given marking stratum have the same probability distribution of movement to the recapture strata; and

5) North and south bank marked fish mix randomly between release at the marking site and capture at the recapture site.

Although Darroch's model allows for spatial and temporal stratification, we had to make assumption 5 because recapture histories of north and south bank fish were linearly dependent resulting in unrealistic abundance estimates, i.e., ones with negative capture probabilities.

Besides providing data to generate a population estimate, sampling procedures at the marking and recapture sites were designed to test these assumptions. A description of these procedures and diagnostic statistical analyses follows.

Marking Site Sampling Procedures

Two-basket fish wheels (wheels) equipped with padded chutes and live holding boxes were used to capture chum salmon at the marking site (Figure 2). Marking wheel baskets were approximately 3.0 m wide and dipped to a depth of 4.5 m below the water's surface. Nylon seine netting was installed on the sides of the baskets to minimize injury to fish as they were lifted clear of the water. Closed cell foam padding was placed along the chute and ramp on the path to the holding boxes to reduce impact injury to fish. Holding boxes were 2.4 m long, 1.2 m deep, and approximately 1 m wide. The walls and floors of the holding boxes contained many 5 cm diameter holes to allow a continuous flow of water while preventing heavy current that could potentially disable weakened fish.

Wheels were placed across from each other on the north and south banks of the river. The river was narrow, deep, and swift in this area making use of large, deep dipping wheels possible. Wheel placement relative to shore was determined by the depth of the dip on the shoreward edge of the baskets. This edge was positioned to sweep within 30 cm of the bottom. Wheels were moved relative to shore as the water level rose or fell to maintain the same proximity to the bottom. A lead, in the form of a submerged picket fence, was placed between the wheel and the shore to direct fish toward the dipping baskets.

Fish were dip netted, handled, and released in a way that minimized stress and trauma. Fall chum salmon were marked with individually numbered spaghetti tags applied with barbed-end applicator needles. We recorded length, sex, tag number, condition and color categories and release times for all marked fish. Length, mid-eye to fork (MEL), was measured to the nearest cm. Sex determination was based on several external indicators, including the condition of the kype and teeth, abdominal distention, the size of the adipose fin, and the condition of the vent.

A condition index was developed to decide which fish received tags and as a means to test for behavioral differences that may accompany a fish's condition. The three condition categories were defined as follows:

Good — fish appeared to have no injuries or fungal infections.

Minor injury — fish had an observable injury such as a cut, an abrasion, or a fungal infection that did not appear to hinder the fish.

Major injury — fish had a deep wound impacting muscle function, torn off gill plate, missing tail, partially destroyed head, an extensive fungal infection that penetrated the dermal layer and exposed muscle tissue, or were bleeding from the gills.

All chum salmon placed in the good and minor injury categories were marked. Those in the major injury category were not marked.

A color index was developed based upon spawning coloration and other secondary spawning characteristics exhibited by individual fish. This index was developed as a possible indicator of distance, either temporal or geographic, to the spawning grounds. The three color categories were defined as follows:

Silver — fish that showed little or no spawning coloration, with vertical barring absent or barely visible in places; and that had pale and translucent pelvic and anal fins; no kype formation; and large, silvery scales dominating the back and sides.

Light — fish that showed definite vertical barring; minimal tooth development; few or no large, silvery scales in males; darkening but somewhat translucent pelvic and anal fins; and that had minimal or developing dorsal humping and kype formation in males, and a firm belly with minimal distention in females.

Dark — fish that were highly colored, with black, red and white vertical barring; and that had opaque black pelvic and anal fins with distinct white tips; extreme tooth development; highly-developed dorsal humping, horizontal flattening, and advanced kype formation in males; and a soft, distended belly in females.

To determine if marked fish retained their tags, secondary marks were applied to all tagged and released fish, August 1-9. A 0.5 cm hole punched in the upper lobe of the caudal fin was used as the secondary mark.

Tagging commenced on August 1 at both marking wheels and ceased on September 19 at the north bank wheel and on September 20 at the south bank wheel. Fish were marked from Monday through Saturday, with no tagging occurring on Sundays. Hours of operation varied throughout the season enabling crews to mark and release ~400 fish per day.

Recapture Site Sampling Procedures

At the recapture site the river was wider and shallower than at the marking site, so the wheels were sized accordingly. Baskets on the recapture wheels were approximately 2.5 m wide and dipped to a depth of 3.0 m below the water's surface. The south bank wheel was placed about 2 km downstream from the north bank wheel.

Recapture procedures were similar to those used for marking. Fish were checked for primary marks while in the dip net, counted, and immediately released. Tag numbers and release times were recorded from recaptured fish. All fish were closely examined for the presence of primary and secondary marks, August 2-9. A tally was kept of the total number of marked and unmarked fish caught.

Sampling commenced at both recapture wheels on August 2 and ceased at the north bank wheel on September 22 and at the south bank wheel on September 20. Recapture wheels were operated 24 hours a day, seven days a week.

Migration Times

We calculated migration times for all fish tagged and released at the marking wheels and caught 50 km upstream in the recapture wheels. Migration time, in days, for each recaptured fish was calculated as

$$\mathit{Migration\ Time} = \frac{(r - g)}{2} - d\ , \tag{1}$$

where r = date and time, to nearest minute, of a marked fish's release at the recapture wheels,

g = date and time, to nearest minute, of the beginning of a sampling period at the recapture wheels, and

d = migration start time, date and time, to nearest minute, of a marked fish's release at the marking wheels.

Since we did not know the exact time of day that fish arrived at the recapture wheels the midpoint, (r - g)/2, was used to estimate the migration end time.

Holding box time (h), in hours, for tagged fish captured at the recapture site, was calculated as

$$h = w - g \tag{2}$$

where w is the date and time, to nearest minute, that a fish was processed at a recapture wheel. Analysis of covariance was used to examine the relationship between estimated migration time and holding box time.

Assessment of Condition and Color Classifications

Assessment of the crew's ability to classify fish by color and condition was done before conducting diagnostic statistical analyses. Color and condition of marked fish recaptured at the marking site was compared with their classification recorded at the time of marking to determine if classifications were consistent.

Diagnostic Statistical Analyses

Diagnostic statistical tests were used to examine the data for violations of the assumptions other than closure. Violation of the closure assumption was unlikely since adult salmon migrate upstream from the ocean to spawn, thus passing the marking site before reaching the recapture site. Further, no fall chum salmon spawning areas are known or suspected to occur between these sites.

Tag retention.— Data on the presence of primary and secondary marks from fish recaptured at the recapture site were used to estimate tag loss between the marking and recapture sites.

Equal probabilities of capture and movement to recapture strata.— Tests could not be developed to determine if 1) all fish had an equal probability of capture at the recapture site or 2) if all fish had the same probability distribution of movement between marking and recapture wheels. Instead we determined if the recapture probabilities, Darroch's R_{ij}'s (i.e., the product of probability of movement to recapture strata, 2_{ij}, and capture probabilities, p_j) were the same for all marked fish of release stratum i. Given that

$$c_{ij} = a_i \, \theta_{ijk} \, p_{rj} = a_i \, \psi_{ij} \, , \tag{3}$$

where c_{ij} = number of marked fish released during week i that were recaptured for the first time during week j (the implicit and untested assumption was that marked and unmarked fish behaved similarly), and

a_i = number of marked fish released during the ith week at the marking site,

we were able to use the recapture data to perform this analysis.

We used multinomial logistic regression, using generalized logits (Agresti 1990), to model the probability of recapture as a function of a fish's sex and length. In choosing a model, we used a likelihood-ratio test to compare the fitted model with a simpler one and then removed parameters one by one until we determined that the fitted model added significant explanatory value over the simpler one. First we started by comparing the full model, i.e., one containing the effects of sex, length, and their interaction, with an intercept only model. The model selection process continued only if the full model was chosen over the intercept only model, i.e., if the likelihood-ratio test statistic, G^2 (full | intercept only), was significant (P # 0.05). Next a comparison was made between the full model and the main effects model, i.e., one containing sex and size. If the test statistic was significant then the main effects model was compared to the best fitting single effect model, i.e., one containing sex or size.

Data collected at the marking and recapture sites were grouped into statistical weeks (Table 1). At the marking site statistical weeks began on Monday and ended on Saturday. At the recapture site statistical weeks began on Tuesday and ended on Monday to allow for migration time. Separate analyses were performed for each marking week, i.e. stratum, because the Darroch estimator is conditioned on them.

Random mixing.— Following Agresti (1990), we used a log-linear model to test if north and south bank marked fish randomly mixed between the marking and recapture sites. We combined data from marking weeks to increase power, but controlled for the effect of the stratum. Combining the data and performing simple 2-factor tests of independence would have led to improper weighting of the data and possibly erroneous conclusions (Christensen 1990). Performing this log-linear analysis, conditioned on statistical week, is analogous to performing the Cochran-Mantel-Haenszel Test.

Abundance Estimate

Following Darroch (1961) we estimated total abundance of unmarked fish for the season, $\hat{n}$, as

$$\hat{n} = b' \, C^{-1} \, a \tag{4}$$

where b and a are vectors and C a matrix such that

$$b = \begin{bmatrix} b_1 \\ b_2 \\ \vdots \\ b_j \\ \vdots \\ b_t \end{bmatrix} \qquad a = \begin{bmatrix} a_1 \\ a_2 \\ \vdots \\ a_i \\ \vdots \\ a_s \end{bmatrix} \qquad C = \begin{bmatrix} c_{11} & c_{12} & \cdots & \cdots & \cdots & c_{1t} \\ c_{21} & c_{22} & \cdots & \cdots & \cdots & c_{2t} \\ \vdots & \vdots & \cdots & \cdots & \cdots & \vdots \\ \vdots & \vdots & c_{ij} & \cdots & \cdots & \vdots \\ \vdots & \vdots & \cdots & \cdots & \cdots & \vdots \\ c_{s1} & c_{s2} & \cdots & \cdots & \cdots & c_{st} \end{bmatrix}, \tag{5}$$

where b_j = number of unmarked fish captured for the first time during the jth week at the recapture wheels,

We estimated b_j by multiplying the total number of unmarked fish captured during week j by the proportion of marked fish recaptured for the first time during week j. The estimate of total abundance, $\hat{N}$, was then calculated as

$$\hat{N} = \hat{n} + \sum a_i \; . \tag{6}$$

Weekly estimates of the number of unmarked fish at the marking site, $\hat{m}_i$, were calculated as

$$\hat{m}' = b'C^{-1}D_a \; , \tag{7}$$

where $\hat{m}$ = vector of the weekly estimates of unmarked fish at the marking site, and

D_a = diagonal matrix whose elements are those of vector a.

Weekly population estimates at the marking site, $\hat{N}_i$, were calculated as

$$\hat{N}_i = \hat{m}_i + a_i \tag{8}$$

and estimates of the probability of capture during marking event i, $\hat{p}_{ci}$, were calculated as

$$\hat{p}_{ci} = \frac{a_i}{\hat{N}_i} \quad . \tag{9}$$

Next we calculated the vector $\hat{\rho}$,

$$\hat{\rho} = C^{-1}a \ . \tag{10}$$

Capture probabilities at the recapture site during stratum j, p_{rj}, were estimated as the reciprocal of the elements of $\hat{\rho}$, i.e.,

$$\hat{p}_{rj} = \frac{1}{\hat{\rho}_j} \quad . \tag{11}$$

The probability that fish marked in stratum i move to stratum j, 2_{ij}, was estimated as

$$\hat{\theta}_{ij} = \frac{c_{ij}}{a_i \, \hat{p}_j} \ . \tag{12}$$

Efron's (1982) bootstrap methods were used to estimate variance and statistical bias for $\hat{N}$, $\hat{N}_i$, $\hat{p}_{ci}$, and $\hat{p}_{rj}$. One thousand Darroch population estimates were generated for fish sampled with replacement from capture histories based on the original data to produce a new set of capture histories. Fish capture histories were defined as

- H_{ij} - fish marked during week i and recaptured for the first time at the recapture site during week j;
- H_{i0} - fish marked during week i but were never recaptured at the recapture site;
- H_{0j} - fish not caught at the marking site but were captured during week j at the recapture site; and,

H^{+}_{ij} - number of recaptures of fish marked during week *i* and recaptured for the second or more times at the recapture site during week *j*.

Bootstrap sample size was equal to the number of tallied capture histories. A bootstrap replicate of the number of fish marked, a^*, was calculated as

$$a^* = \begin{bmatrix} H_{10} + \sum_{j=1}^{t} H_{1j} \\ H_{20} + \sum_{j=1}^{t} H_{2j} \\ \vdots \\ H_{i0} + \sum_{j=1}^{t} H_{ij} \\ \vdots \\ H_{s0} + \sum_{j=1}^{t} H_{sj} \end{bmatrix}. \tag{14}$$

The number of recaptured fish, C^*, was calculated as

$$C^* = \begin{bmatrix} H_{11} & H_{12} & \cdots & \cdots & \cdots & H_{1t} \\ H_{21} & H_{22} & \cdots & \cdots & \cdots & H_{2t} \\ \vdots & \vdots & \cdots & \cdots & \cdots & \vdots \\ \vdots & \vdots & H_{ij} & \cdots & \cdots & \vdots \\ \vdots & \vdots & \cdots & \cdots & \cdots & \vdots \\ H_{s1} & H_{s2} & \cdots & \cdots & \cdots & H_{st} \end{bmatrix}. \tag{15}$$

And, the number of unmarked fish captured for the first time, b^*, was calculated as

$$b^* = \begin{bmatrix} H_{01}\left(\dfrac{\sum_{i=1}^{s} H_{i1}}{\sum_{i=1}^{s} H_{i1}+H_{i1}^{+}}\right) \\ H_{02}\left(\dfrac{\sum_{i=1}^{s} H_{i2}}{\sum_{i=1}^{s} H_{i2}+H_{i2}^{+}}\right) \\ \vdots \\ H_{0j}\left(\dfrac{\sum_{i=1}^{s} H_{ij}}{\sum_{i=1}^{s} H_{ij}+H_{ij}^{+}}\right) \\ \vdots \\ H_{0t}\left(\dfrac{\sum_{i=1}^{s} H_{it}}{\sum_{i=1}^{s} H_{it}+H_{it}^{+}}\right) \end{bmatrix}. \tag{16}$$

Statistical bias for each estimated parameter was calculated as the mean of the estimates generated from the bootstrap samples minus the actual estimate. Variance was estimated as the variance of the sample of estimates generated for each parameter.

Bias

We modeled the fall chum salmon run in two ways to determine the sensitivity of the Darroch population estimator to violations of the assumptions. This modeling was done for two reasons. First, we made some untestable assumptions about the data. Second, test results indicated violations of assumptions about movement to the recapture weeks and/or capture probabilities in recapture weeks.

Bias associated with violations of assumptions about movement to recapture weeks and/or capture probabilities in recapture weeks was evaluated as follows. We calculated expected values for a_i, c_{ij} and b_j based on specified values of N_i, p_{ci}, θ_{ij}, and p_{rj} and weekly sex ratios. The expected number of fish marked during week *i*, a_i , was calculated as

$$a_i = \sum_{k=1}^{2} N_i \, p_{ik} \, p_{cik} \tag{17}$$

where p_{ik} is the proportion of the N_i migrants of sex *k* fish during marking week *i*, and p_{cik} is the probability of capture of sex *k* fish during marking week *i*. Next the expected number of fish released during marking week *i* that were recaptured for the first time during recapture week *j*, c_{ij}, was calculated as

$$c_{ij} = \sum_{k=1}^{2} N_i \, p_{ik} \, p_{cik} \, \theta_{ijk} \, p_{rjk} \tag{18}$$

where, θ_{ijk} is the probability that fish of sex *k* marked during week *i* move to recapture week *j* and p_{rjk} is the probability of capture of sex *k* during recapture week *j*. Lastly, the expected number of unmarked fish captured during week *j*, b_j, was calculated as

$$b_j = \sum_{i=1}^{s} \sum_{k=1}^{2} N_i \, p_{ik} \, (1 - p_{cik}) \, \theta_{ijk} \, p_{rjk} \tag{19}$$

We then varied p_{ci} and p_{rj} for male and female fish such that the odds of males being captured was 0.8 to 2.0 times that of females. The odds of an event occurring, *O,* are defined as

$$O = \frac{p}{1-p} \tag{20}$$

where p is the probability of that event occurring. We also varied the migration parameter, θ_{ij}, such that the odds of males being recaptured during their marking week was equal to or ten times greater than that of females. For each combination of p_{cik}, p_{rjk}, and θ_{ijk}, we used Darroch's model to estimate N_i and to calculate bias.

We used Monte-Carlo simulations to investigate how specific characteristics of our study design potentially affected our estimates. In our simulations, individual fish migrated through the study area from marking week *i* to recapture week *j* with values of N_i, p_{ci}, p_{rj}, and movement parameters, 2_{ij}, from marking week *i* to recapture week *j* equal to point estimates from our experiment. The number of fish passing the marking site each day of the *i*th week was equal to $N_i / 7$. Whether a fish was marked or not was modeled as a Bernoulli trial with probability p_{ci}. Movement to the recapture site, in days, was modeled as a multinomial random variable based on weekly distributions of migration times estimated from recaptured fish. Capture of each fish at the recapture site was treated as a Bernoulli trial with probability p_{rj}. Daily capture histories were then tabulated according to marking and recapture week to obtain modeled replicates of a_i, c_{ij}, and b_j.

Each simulated tagging experiment was repeated 500 times. Darroch's model was used to estimate N, N_i, p_{ci}, and p_{rj} for each repetition. Standard errors and bias were estimated for each experiment. Bias was calculated as the mean of the simulations minus the modeled value and standard errors equaled the standard deviations of the estimates.

The first simulation acted as the baseline for making comparisons. In this scenario fish were tagged at the marking site 7 days per week, captured at the recapture site 7 days per week, and tagged and untagged fish moved to the recapture site at the same rate. In the second simulation, fish were marked during the first 6 days of each week as in our experiment. This simulation was used to examine the effect of our 6 day marking protocol on the bias of the estimate. In the third simulation, a variation on our 6 day marking protocol, fish were marked during the last 6 days of each statistical week. In the last simulation, all tagged fish moved to the recapture site at the rate determined from our experiment, but all untagged fish reached the recapture site in 1 day. We did this simulation because we had to make the untestable assumption that marked and unmarked fish had the same weekly probability distribution of movement past the recapture site. We felt the simulated differential movement was a worst case scenario; capturing, holding, and tagging fish was more likely to delay, than accelerate, movement of fish to the recapture site upon release; and few untagged fish that passed the marking site were likely to reach the recapture site in < 1 day.

Results

From August 1 through September 21, 1996, 17,751 fall chum salmon were tagged at the marking wheels. Lengths of tagged fish ranged from 49 to 74 cm MEL. Males made up 52% and females 48% of the tagged fish. A total of 191 fish, ~1%, were classified as having major injuries and were released without marking. From August 2 to September 23, 45,232 fall chum salmon were examined for primary marks at the recapture wheels. Excluding multiple recaptures, 1,259 marked fish were recaptured. On average, fewer than 10% of the fish were recaptured more than once (Table 2).

Migration Times

Modes of estimated migration times for tagged fish were 1 day in each statistical week (Figure 3). However, the variation in estimated migration time decreased from statistical week 1 to 8. Ninety-percent of tagged fish released during week 1 took < 4.3 days to reach the recapture wheels, whereas 90% of the tagged fish released during week 8 took < 2 days to reach the recapture wheels. Mean estimated migration time differed between the sexes (Table 3). In six of the eight weeks males took less time than females to reach the recapture site.

Holding box times for recaptured tagged fish, i.e., the time elapsed between the beginning of a sampling period and the time an individual fish was released, averaged 8.1 hours (Table 4) and ranged from 5.8 hours during week 6 to 10.1 hours during week 2. The relationship between estimated migration time and holding time varied among weeks (Table 5). Estimated migration times decreased 0.04 days per hour of holding time during week 2, but increased 0.23 days per hour of holding time in week 7 (Table 5).

Assessment of Condition and Color Classifications

Inconsistencies were detected during examination of condition and color data from 1,092 tagged fish recaptured at the marking wheels (Tables 6-7). Approximately 2% of the fish classified as in good condition during marking were classified differently upon recapture at the marking wheels (Table 6). Fish initially classified as injured were assigned different condition 41% of the time. For color, 5%, 54% and 40% of the fish were originally classified as silver, light and dark, respectively (Table 7). Of these, 44%, 18% and 30% were assigned to different categories during the second examination. Due to these inconsistencies we eliminated condition and color from further analyses.

Diagnostic Statistical Analyses

Tag retention.— No evidence of tag loss was observed. Between August 1 and 9, a total of 2,752 fall chum salmon were released with primary and secondary marks at marking wheels. At the recapture wheels, 210 fish were found to have secondary marks, all of which had primary marks.

Equal probabilities of capture and movement to recapture strata.— Results of the logistic regressions of capture histories on size and sex indicate that the probabilities of recapture in weeks 3, 5, 7, and 8 were independent of these characteristics (Table 8). During weeks 1 and 6 the odds of being recaptured were associated with a fish's size. An interaction effect between size and sex affected the probability of recapture in week 2. Week 4 was the only week in which the odds of being recaptured were associated solely with the sex of a fish.

Based on the parameter estimates from the logistic regression analyses (Table 9), we estimated that small tagged fish (for example 55 cm MEL) released during week 1 were twice as likely of being captured during recapture week 1 at the recapture site as were large tagged fish (e.g., 65 cm MEL). Conversely, small tagged fish released during week 1 were half as likely of being captured at the recapture site during recapture week 2, the week following marking, than were large fish.

The probabilities changed for fish marked during week 2 such that the odds of being recaptured at the recapture site during week 2 were 1.8 times higher for small females than large females, but 2.2 times higher for large males than small males. By week 3, large females marked during week 2 were 3.7 times more likely to be recaptured at the recapture site than small females whereas small males marked during week 2 were twice as likely to be recaptured than large males.

Of the fish marked during week 4, the odds of being recaptured at the recapture site were 1.9 times higher for males than females during week 4, but only 1.2 times higher during week 5. Lastly, large fish marked during week 6 were 1.6 times more likely to be recaptured at the recapture site during week 6 as small fish but just as likely as small fish to be recaptured during week 7.

Random mixing.— Marked fish randomly mixed between release at the marking site and recapture at the north and south bank recapture wheels (Log-linear model, $G^2 = 5.04$, $P = 0.75$; Table 10). This evidence supports the assumption of random mixing, thereby making stratification by bank unnecessary.

Abundance Estimate

Due to the detected assumption violations, abundance estimates based on sex and/or size should have been generated. Instead an abundance estimate independent of sex and size was generated, then simulations were carried out to investigate bias.

We estimated that 654,296 ± 41,956 (95% C.I.) fall chum salmon migrated past the marking site during the course of the study (Table 11). Weekly estimates at the marking site ranged from a minimum of 14,768 ± 2,989 (95% C.I.) during week 1 to a maximum of 126,268 ± 20,164 (95% C.I.) during week 4 (Table 12). Estimated capture probabilities at the marking site were highest at the start of the study and lowest at the end of the study. Because the recapture wheels were operated for a longer period each day compared to the marking wheels, weekly capture probabilities were higher at the recapture site (range: 0.026 - 0.140) than at the marking site (range: 0.015 - 0.073).

Bootstrap precision of population estimates and capture probabilities was high. For seven of the eight weekly estimates the coefficient of variation (CV) was less than 11% (Table 12). Precision was poorest for estimates generated at the beginning and end of the season, the times when the number of recaptures was lowest (Table 2). Estimated statistical bias was low and usually < ±1% (Table 12). All 1,000 bootstrap samples produced reasonable capture probability estimates at the marking and recapture sites, i. e. they all fell within the range 0-1.

Bias

The effect of differential probability of capture between the sexes on the bias of weekly and total population estimates depended on its cause. The observed differences could have been due to differential probabilities of capture, to differential movement rates between the marking and recapture sites, or a combination of the two (Table 13).

For the baseline we modeled the situation in which male and female fish had the same probability of capture and movement rates. Bias was absent as expected. Absolute bias increased as males were less, or more, likely to be captured relative to females and ranged from negative to positive as males became more vulnerable to capture (Table 13). However, for any given odds ratio, based on the capture probabilities of male and female fish, the change in bias was negligible when males moved to the recapture wheels faster than females.

Bias was low for population estimates under simulated baseline conditions of the 1996 fall chum salmon run. In these simulations fish were marked and recaptured seven days a week, with marked and unmarked fish moving to the recapture site at the same rate (Table 14). Weekly bias was positive and less than 2% and seasonal bias was only 0.6%.

Bias of population estimates increased compared to the baseline in the tagging project simulation in which fish were tagged during the first six days of each week (Table 15). Absolute bias was largest during the first (-9.9%) and last (7.6%) weeks of this simulation, the weeks when the number of marked fish at the recapture wheels was lowest. Generally, bias ranged from negative to positive values during the season. Shifting the tagging to the last six days of each week reduced the maximum absolute bias to less than that of tagging during the first six days of each week (Table 16). A decline in bias occurred over the season. Seasonal bias was only 0.8%.

The increase in bias was negligible in simulations in which fish were marked during the first six days of each week and all untagged fish reached the recapture site in 1 day (Tables 15 and 17). Allowing untagged fish to reach the recapture wheels before tagged fish did not increase bias of the total population estimate. Weekly estimates of bias for N_i, p_{ci}, and p_{rj} increased <1.6 % during all weeks in this simulation, compared to results from the simulation in which tagged and untagged fish traveled to the recapture site at the same rate.

Discussion

We estimated that a total of 654,296 fall chum salmon migrated up the Yukon River past our marking site near the village of Rampart. Although diagnostic tests demonstrated that some assumptions underlying this estimate were violated, our estimate agrees reasonably well with upriver escapement and harvest estimates. The estimated 1996 fall chum escapements for the Chandalar, Sheenjek, and Fishing Branch rivers and the Canadian mainstem Yukon River totaled 651,614 fish (JTC 1996). These monitoring sites are believed to represent most of the fall chum salmon run above our study area. The total estimated 1996 U. S. and Canada commercial and subsistence fall chum harvest above our study area was 57,198 fish (JTC 1996; Busher 1997; Alaska Department of Fish and Game, unpublished data). Combined escapement and harvest estimates total 708,812 fall chum salmon, about 8% more than our tagging estimate.

Several concerns need to be addressed when evaluating our population estimate. The simplest to address is bias due to our statistical marking week definition. Our simulations showed that season bias was nearly identical whether fish were tagged during the last six days of a statistical week (0.8%), the first six days of each week (0.5%), or when fish were tagged every day. Thus we can conclude that our marking week definition has a negligble effect on bias.

More problematic are those concerns associated with violations of the model assumptions. One basic assumption is that marks are not lost (Ricker 1975; Everhart and Young 1981; Van Den Avyle 1993; Arnason et al. 1996). Pahlke and Bernard (1996) reported high spaghetti tag loss for chinook salmon recaptured on spawning grounds in the Taku River drainage. However, tag loss has been observed during territorial fighting on spawning grounds among fall chum salmon (S. Maclean, U. S. Geological Service, Biological Resources Division, personal communication). Milligan et al. (1986) reported that the assumption of no tag loss was met in a tagging study of fall chum salmon in the Canadian portion of the Yukon River in which fish traveled from 300 to 800 km prior to recapture, but no quantitative method was used to evaluate tag retention.

In our study, from August 1 through August 9, tag loss was not detected between lower and upper wheels. We believe that this occurred because time and distance between mark and recapture were minimized (Eder 1990; Cappiello and Bromaghin 1996). Logically, tag loss should increase as time or distance between sampling events increases (McGregor et al. 1991; Fabrizio et al. 1996). Tag loss should be highest in studies where salmon are tagged as they enter freshwater and are recovered at distant spawning grounds. In contrast, our study limited the minimum travel distance to approximately 50 km and travel time was usually less than two days.

Violations of the assumptions for capture probabilities at the recapture site and rate of movement are also a concern. Ryan (1990) found size selective sampling was actually due to differential habitat use and the amount of movement by various salmonid size groups. During some weeks of our study we detected the violation of these assumptions. However, results from the logistic regressions can only be used as a guide in determining if the assumptions about capture probabilities at the recapture site and movement to recapture strata were satisfied. Because R_{ij} is the product of capture probabilities and movement rates, situations could occur such that the p_j's and 2_{ij}'s differ with sex and/or size, but the R_{ij}'s do not. The end result is that tests may fail to detect violations of the assumptions about capture probabilities and movement distributions regardless of sample size.

Given these violations, we should have generated separate estimates for each sex and/or size class (Milligan et al. 1986; Bernard and Hansen 1992). However, we could not do so because we did not know the sex or size of unmarked fish captured at the recapture site.

Results from logistic regressions were used to detect and quantify violation of the assumptions about capture probabilities at the recapture site and rate of movement to recapture strata and to design simulation studies to evaluate probable effects on the population estimate. In our simulations the potential bias from violations appeared to be negligible. Bias was low in simulations where males were ten times more likely than females to move to the recapture site in the week in which they were marked or when untagged fish moved to the recapture site at a faster rate than tagged fish.

The effect of these violations was minimized by the migration speed. Most of the fish in our study were recaptured during the statistical week in which they were marked and migration accelerated as the season progressed. On average tagged fish reached the recapture site 1.4 to 2.6 days after being tagged and released therefore most fish were recaptured in the week they were marked.

Sex differences in migration timing fit the pattern of recapture probabilities. Tagged males took less time than females to reach the recapture site and males were more likely than females to be recaptured in the week they were tagged. Therefore, the differential odds of being recaptured between males and females were due, at least in part, to differential rates of movement to recapture strata rather than selective sampling. If the differences in the odds of being recaptured were due solely to differential movement to recapture week, our modeling efforts imply that the bias of the population estimates is low.

A method, developed by Schwarz and Dempson (1994), allows for differential capture probability on a day to day basis and can be used to test if data can be pooled to calculate the Darroch population estimate. An advantage to this method is that tagged and untagged fish are not assumed to reach the recapture site at the same rate. However, the Schwartz and Dempson model requires accurate data on migration timing. Our data could not be used with this model because holding box times were long and highly variable preventing accurate estimation of migration time.

Fish condition and spawning color were characteristics potentially indicative of the salmon stocks migrating through our study area and were expected to affect the rate of movement to recapture strata. Comparisons using fish recaptured at the marking wheels indicated problems in consistent classification of condition and color. Condition and color classifications were done in an arbitrary manner and post-season debriefings indicated that crews felt definitions of each changed with time. This change was partly due to experience gained while sampling. Also contributing to this change was the lack of strict criteria for crews to use in their classification of individual fish. Three results from our findings were considered. First, better guidelines can be set for future studies. Second, experienced observers from 1996 can train new observers, thus making classifications among individuals more consistent. Third, some inconsistencies in condition and color classification will remain and new models to account for such discrepancies must be developed before condition and color can be used in population estimation. We plan to collect these data in 1997 to determine if more consistent assessments of condition and color are possible.

The assumption of random mixing of marked fish between the marking and recapture sites was our last concern. Some studies have demonstrated bank fidelity for salmon stocks migrating in sections of large rivers (Buklis 1981; Buklis and Barton 1984; Milligan et al. 1986, Spearman and Miller 1997). In some cases this behavior is associated with the confluence of a tributary (Buklis and Barton 1984; Milligan et al. 1986). In our study the recorded changes between river banks indicated at least one crossing of the river by some marked fish (north to south or south to north). Telemetry data observations (J. Eiler, National Marine Fisheries Service, personal communication) indicated that some fall chum salmon which resumed upstream movement switched banks.

Bank fidelity on the Yukon River described by both Buklis and Barton (1984) and Spearman and Miller (1997) occurred below the Tanana River, a major tributary and origin of several large chum salmon stocks (Barton 1992). The lack of bank fidelity demonstrated by our study may be the result of the great distance between our sampling area and the next major tributary upstream. In addition, most stocks above the Tanana River pass through the Yukon Flats, an area characterized by more than 400 km of shallow and braided channels. Bank fidelity would probably not be relevant to homing in a highly braided channel far from the river of origin for an individual.

In conclusion, our results demonstrate estimation of weekly and total run abundances of fall chum salmon in the upper Yukon River is feasible. The variations in the odds of recapture of individuals were probably due to differential migration rates rather than sampling selectivity. Our sampling design will be modified to increase our ability to more definitively address bias.

Recommendations

1. Continue to use the Darroch model, possibly with stratification, to estimate the abundance of fall chum salmon on the upper Yukon River.

2. At the marking site provide clear criteria for use in classifying marked fish by condition and color.

3. Continue to evaluate the marking site crew’s ability to consistently classify marked fish by condition and color.

4. Collect additional data at the recapture site to enable stratification of population estimates by size, sex, condition and color, if necessary.

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Table 1.— Sampling dates of fall chum salmon migrating past the marking and recapture sites on the Yukon River, Alaska, August 1 to September 24, 1996. At the marking site weeks were started on Monday and concluded on Saturday. At the recapture site weeks were started on Tuesday and concluded on Monday to allow for migration. All dates are inclusive.

	Sampling dates	
Statisical week	Marking site	Recapture site
1	August 1 - August 3	August 1 - August 3
2	August 5 - August 10	August 6 - August 12
3	August 12 - August 17	August 13 - August 19
4	August 19 - August 24	August 20 - August 26
5	August 26 - August 31	August 27 - September 2
6	September 2 - September 7	September 3 - September 9
7	September 9 - September 14	September 10 - September 16
8	September 16 - September 21	September 17 - September 23

Table 2.— Weekly capture histories of tagged fall chum salmon migrating past the marking and recapture sites on the Yukon River, Alaska, August 1 to September 24, 1996.

Marking week, i	Marked fish released, a_i	Recapture week, j								Fish not recaptured
		1	2	3	4	5	6	7	8	
		Recaptured the first time								
1	1,041	75	46	1	0	0	0	0	0	919
2	2,108	0	134	42	1	0	0	0	0	1,931
3	2,771	0	0	155	18	2	0	0	0	2,596
4	2,766	0	0	0	148	14	1	0	0	2,603
5	2,820	0	0	0	0	196	13	1	0	2,610
6	2,704	0	0	0	0	0	215	8	1	2,480
7	2,473	0	0	0	0	0	0	141	2	2,330
8	1,068	0	0	0	0	0	0	0	28	1,040
Estimated unmarked fish, b_j		989	2,309	5,628	7,211	7,151	9,435	6,510	1,919	
		Previously recaptured								
1		8	2	2	0	0	0	0	0	
2		0	10	3	0	0	0	0	0	
3		0	0	13	0	0	0	0	0	
4		0	0	0	6	2	0	0	0	
5		0	0	0	0	11	3	0	0	
6		0	0	0	0	0	9	0	0	
7		0	0	0	0	0	0	9	2	
8		0	0	0	0	0	0	0	2	
Total unmarked fish		1,094	2,463	6,140	7,470	7,590	9,929	6,901	2,167	
Percent first recaptures		90.4	93.8	91.7	96.5	94.2	95.0	94.3	88.6	

Table 3.— Mean estimated migration time (d) for tagged fall chum salmon between the marking and recapture sites, by statistical week and sex, on the Yukon River, Alaska, August 1 to September 24, 1996.

Marking week, *k*	Sex	*N*	Mean
1	Females	59	2.7
	Males	63	2.5
	Combined	122	2.6
2	Females	72	3.0
	Males	105	2.6
	Combined	177	2.8
3	Females	67	2.1
	Males	108	2.1
	Combined	175	2.1
4	Females	50	1.9
	Males	113	1.6
	Combined	163	1.7
5	Females	93	1.6
	Males	117	1.7
	Combined	210	1.6
6	Females	108	1.4
	Males	115	1.3
	Combined	223	1.3
7	Females	72	1.6
	Males	71	1.3
	Combined	143	1.5
8	Females	22	1.4
	Males	7	1.1
	Combined	29	1.4

Table 4.— Mean, 5th-, 50th-, and 95th-percentile of holding box times (date and time an individual fish was processed minus the date and time of wheel startup for a given sampling period), in hours, of tagged fall chum salmon caught in recapture wheels, on the Yukon River, Alaska, August 1 to September 24, 1996.

Recapture week	*N*	Mean (hr)	SD	Percentiles 5%	50%	95%
1	122	9.6	3.2	4.3	11.0	14.5
2	177	10.1	3.1	4.5	11.0	13.8
3	170	9.2	6.5	4.3	7.8	29.5
4	163	8.4	5.4	4.3	7.5	12.5
5	210	7.3	2.4	4.3	6.8	11.3
6	224	5.8	3.2	2.3	5.5	8.5
7	146	7.2	1.8	3.8	7.3	10.0
8	27	9.4	2.5	4.8	10.3	11.8
Overall	1,239	8.1	4.2	4.0	7.5	13.3

Table 5.— Analysis of covariance table, and model parameter estimates, from test of effect of estimated holding box time (h) in recapture wheels and marking stratum (statistical week) on estimated migration time (d) of tagged fall chum salmon in recapture wheels, on the Yukon River, Alaska, August 1 to September 24, 1996.

Source	df	Sum of squares	Mean square error	F	*P*-value
Model	15	435.8	29.1	10.2	0.0001
Marking stratum	7	106.9	15.3	5.4	0.0001
Holding box time	1	15.1	15.1	5.3	0.02
Tagging stratum x holding box time interaction	7	36.6	5.2	1.8	0.08
Error	1223	3471.6	2.8		
Corrected total	1238	3907.5			

Parameter	Estimate	SE	CV
Intercept	1.11	1.27	1.14
Week 1	0.71	1.36	1.92
Week 2	2.03	1.35	0.67
Week 3	1.00	1.29	1.29
Week 4	0.53	1.30	2.45
Week 5	0.10	1.33	13.30
Week 6	-0.06	1.30	21.67
Week 7	-1.65	1.40	0.85
Holding box time	0.03	0.13	4.33
Holding box time x week 1	0.05	0.14	2.80
Holding box time x week 2	-0.07	0.14	2.00
Holding box time x week 3	-0.03	0.13	4.33
Holding box time x week 4	-0.03	0.13	4.33
Holding box time x week 5	0.03	0.14	4.67
Holding box time x week 6	0.01	0.14	14.00
Holding box time x week 7	0.20	0.15	0.75

Table 6.— Consistency of condition classification of fall chum salmon marked and recaptured in marking wheels on the Yukon River, Alaska, August 1 to September 24, 1996.

	Recapture assessment (row %)		
Marking assessment	Good	Minor injury	Total
Good	1,020 (98)	18 (2)	1,038
Minor injury	22 (41)	32 (59)	54
Total	1,042	50	1,092

Table 7.— Consistency of color classification of fall chum salmon marked and recaptured in marking wheels on the Yukon River, Alaska, August 1 to September 24, 1996.

	Recapture assessment (row %)			
Marking assessment	Silver	Light	Dark	Total
Silver	33 (56)	26 (44)	0 (0)	59
Light	19 (3)	487 (82)	89 (15)	595
Dark	1 (0.2)	133 (30)	304 (69)	438
Total	53	646	393	1,092

Table 8.— Results of logistic regressions of capture histories on size, mid-eye to fork length (cm), and sex of fall chum salmon migrating past the marking and recapture wheels on the Yukon River, Alaska, August 1 to September 24, 1996. Comparisons are between the intercept (no characteristics included) and full (size, sex, and the interaction) models, the full and main effects (size and sex) models, and between the main effects and best single effect (size or sex) models. G^2 is the likelihood ratio test statistic used in the comparison of the models of the effect of these characteristics on the probability of recapture in recapture weeks $j = i$ and $j = i + 1$.

Marking week, i	Logistic regression model -2 log likelihood			G^2	df	P
	Intercept		**Full**			
1	915.07		902.74	12.34	6	0.05
2	1411.61		1391.44	20.16	6	<0.01
3	1430.41		1423.18	7.23	6	0.30
4	1339.38		1318.99	20.40	6	<0.01
5	1597.73		1591.51	6.22	6	0.40
6	1620.30		1604.28	16.02	6	0.01
7	1092.77		1090.58	2.18	3	0.53
8	259.17		255.26	3.12	3	0.27
	Main effects		**Full**			
1	904.41		902.73	1.67	2	0.43
2	1403.54		1391.44	12.10	2	<0.01
4	1324.39		1318.99	5.40	2	0.07
6	1605.40		1604.28	1.12	2	0.57
	Best single effect					
	Sex	**Size**	**Main effects**			
1		906.44	904.41	2.03	2	0.36
4	1327.48		1324.39	3.09	2	0.21
6		1605.44	1605.40	0.05	2	0.98

Table 9.— Parameter estimates from the logistic regression of capture histories on size, mid-eye to fork length (MEL), and sex of fall chum salmon migrating past the marking and recapture wheels on the Yukon River, Alaska, August 1 to September 24, 1996. In the fitted model, when $k = 0$, Pr = probability that a marked fish was not recaptured; when $k = 1$, Pr = probability that a marked fish was recaptured during week $j = i$; and when $k = 2$, Pr = probability that a marked fish was recaptured during week $j = i + 1$. $SEX = 1$ for females and $SEX = -1$ for males. $\alpha_0 = \beta_{10} = \beta_{20} = \beta_{30} = 0$.

Marking week, i	Parameter estimates							
	α_1	α_2	β_{11}	β_{12}	β_{21}	β_{22}	β_{31}	β_{32}
1	1.74	-6.60	-0.07	0.06	-	-	-	-
2	-3.57	-5.46	0.01	0.03	3.95	-5.71	-0.07	0.10
3	-	-	-	-	-	-	-	-
4	-2.95	-5.17	-	-	-0.31	-0.08	-	-
5	-	-	-	-	-	-	-	-
6	-5.61	5.22	0.05	-0.18	-	-	-	-
7	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	-

Fitted model - $$Pr\{recapture\,history = k\} = \frac{e^{(\alpha_k + \beta_{1k}\,MEL + \beta_{2k}\,SEX + \beta_{3k}\,MEL\ SEX)}}{\sum_{h=0}^{2} e^{(\alpha_h + \beta_{1h}\,MEL + \beta_{2h}\,SEX + \beta_{3h}\,MEL\ SEX)}}$$

Table 10.— River bank capture histories of tagged Yukon River fall chum salmon at the marking and recapture sites, August 1 to September 24, 1996.

		Recaptured fish (row %)	
Marking week	Marking bank	North bank	South bank
1	North	31 (39)	49 (61)
	South	16 (38)	26 (62)
2	North	29 (28)	73 (72)
	South	32 (43)	43 (57)
3	North	40 (41)	58 (59)
	South	34 (44)	43 (56)
4	North	45 (44)	57 (56)
	South	27 (44)	34 (56)
5	North	60 (40)	90 (60)
	South	27 (45)	33 (55)
6	North	77 (45)	93 (55)
	South	22 (41)	32 (59)
7	North	42 (38)	69 (62)
	South	13 (41)	19 (59)
8	North	3 (16)	16 (84)
	South	1 (11)	8 (89)

Table 11.— Population estimate ($\hat{N}$) of fall chum salmon migrating past the marking and recapture sites on the Yukon River, Alaska, August 1 to September 24, 1996. & = mean of 1000 bootstrap estimates and % Bias = (difference between mean of bootstrap estimates and estimated value) / estimated value. Bootstrap estimates based on 1000 iterations.

$\hat{N}$	&	SE	CV	% Bias
654,296	658,891	21,351	0.032	0.70

Table 12.— Weekly population estimates ($\hat{N}_i$) of fall chum salmon migrating past the marking site on the Yukon River, Alaska, August 1 to Sep24, 1996. $\&_i$ = mean of bootstrap estimates, Bias = Bias / $\&_i$, $\hat{p}_{ci}$ = estimated marking site capture probability, $\bar{p}_{ci}$ = mean marking site capture probability from bootstrap estimates, $\hat{p}_{rj}$ = estimated recapture site capture probability, $\bar{p}_{rj}$ = mean recapture site capture probability from bootstrap estimates, % Bias = (difference between mean of bootstrap estimates and estimated value)/estimated value. Bootstrap estimates based on 1000 iterations.

	Statistical week							
	1	2	3	4	5	6	7	8
				Population estimate				
$\hat{N}_i$	14,768	28,889	93,610	126,268	95,770	115,415	110,225	69,350
$\&_i$	14,895	29,012	93,791	126,843	96,185	115,775	110,760	71,630
SE	1,521	2,981	7,207	10,262	6,709	7,752	9,546	13,087
CV	0.102	0.103	0.077	0.081	0.070	0.067	0.086	0.183
% Bias	0.9	0.4	0.2	0.5	0.4	0.3	0.5	3.3
				Probability of capture at marking site				
$\hat{p}_{ci}$	0.070	0.073	0.030	0.022	0.029	0.023	0.022	0.015
$\bar{p}_{ci}$	0.071	0.073	0.030	0.022	0.029	0.023	0.022	0.015
SD	0.007	0.008	0.002	0.002	0.002	0.002	0.002	0.003
CV	0.104	0.105	0.079	0.081	0.071	0.068	0.087	0.176
% Bias	0.3	0.5	0.3	0.1	0.1	0.1	0.2	-0.2
				Probability of capture at recapture site				
$\hat{p}_{rj}$	0.140	0.094	0.064	0.058	0.074	0.085	0.059	0.026
$\bar{p}_{rj}$	0.147	0.094	0.064	0.058	0.074	0.085	0.059	0.026
SD	0.037	0.012	0.005	0.005	0.005	0.006	0.005	0.005
CV	0.250	0.125	0.086	0.081	0.071	0.074	0.085	0.184
% Bias	4.7	0.30	0.6	0.2	0.0	0.5	0.3	-0.3

Table 13.— Percent bias of weekly and total population estimates of fall chum salmon migrating past the marking and recapture sites on the Yukon River, Alaska, August 1 to September 24, 1996. Conditions of capture are when the odds ratio of recapture ranged from 0.8 to 2.0 times higher for males than for females. Eq = males and females travel between sites at the same speed. Un = males are 10 times more likely than females to reach the recapture site in the same week as marking.

	Odds ratio of males:females											
	0.8		0.9		1.0		1.1		1.2		2.0	
Marking week, *i*	Eq	Un	Eq	Un	Eq	Un	Eq	Un	Eq	Un	Eq	Un
1	-8.0	-7.6	-4.0	-3.8	0.0	0.0	4.0	3.9	8.0	7.7	39.0	37.7
2	-10.6	-13.4	-4.9	-6.4	0.0	0.0	4.1	5.7	7.6	10.7	20.3	33.5
3	-12.3	-12.4	-5.7	-5.8	0.0	0.0	4.9	4.9	9.0	9.1	24.5	24.7
4	-10.5	-9.8	-5.2	-4.9	0.0	0.0	5.3	4.9	10.5	9.7	52.0	48.1
5	-9.8	-9.8	-4.9	-4.9	0.0	0.0	4.9	4.9	9.8	9.8	48.6	48.4
6	-8.7	-8.7	-4.4	-4.4	0.0	0.0	4.4	4.4	8.7	8.7	43.6	43.6
7	-8.3	-8.3	-4.2	-4.2	0.0	0.0	4.2	4.2	8.3	8.3	41.3	41.3
8	-6.7	-6.6	-3.3	-3.3	0.0	0.0	3.3	3.3	6.7	6.6	33.0	33.0
Total	-9.5	-9.5	-4.7	-4.7	0.0	0.0	4.5	4.5	8.9	8.9	40.6	40.4

Table 14.— Results of the baseline Monte Carlo simulation of the fall chum salmon migrating past the marking and recapture sites on the Yukon River, Alaska, August 1 to September 24, 1996. The baseline conditions represent the optimal situation where fish are tagged 7 days a week and marked and unmarked fish move to the recapture strata at the same rate. N_i, N, p_{ci}, p_{rj} are modeled values of the population estimates and capture probabilities. $\bar{N}_i$, $\bar{p}_{ci}$, $\bar{p}_{rj}$ are based on 500 bootstrap estimates.

	Statistical week							
	1	2	3	4	5	6	7	8
N_i	14,763	28,889	93,604	126,266	95,767	115,409	110,222	69,349
$\bar{N}_i$	14,843	29,115	94,717	127,097	96,367	115,445	110,194	70,710
SE	1,282	2,309	7,693	10,133	7,435	7,384	8,990	16,273
% Bias	0.5	0.8	1.2	0.7	0.6	0.0	0.0	2.0
P_{ci}	0.070	0.073	0.030	0.022	0.029	0.023	0.022	0.015
$\bar{P}_{ci}$	0.070	0.073	0.029	0.022	0.029	0.023	0.023	0.015
SD	0.006	0.006	0.002	0.002	0.002	0.002	0.002	0.003
% Bias	0.0	0.0	-0.5	0.1	-0.1	0.2	0.5	-0.1
p_{rj}	0.140	0.094	0.064	0.058	0.074	0.085	0.059	0.026
$\bar{p}_{rj}$	0.141	0.093	0.064	0.058	0.074	0.085	0.059	0.026
SD	0.015	0.008	0.005	0.005	0.005	0.005	0.005	0.005
% Bias	0.3	-0.2	-0.3	-0.1	-0.1	0.3	1.0	-0.2
Total	N = 654,269 $\bar{N}_i$ = 658,488 SE = 23,501 % Bias = 0.6							

Table 15.— Results of the second Monte Carlo simulation of the fall chum salmon migrating past the marking and recapture sites on the Yukon River, Alaska, August 1 to September 24, 1996. In this simulation, fish were tagged at the marking site during the first six days of each statistical week. N_i, $\underline{N}$, p_{ci}, p_{rj} are modeled values of the population estimates and capture probabilities. $\bar{N}_i$, $\bar{p}_{ci}$, $\bar{p}_{rj}$ are based on 500 bootstrap estimates.

	Statistical week							
	1	2	3	4	5	6	7	8
$\underline{N}_i$	14,763	28,889	93,604	126,266	95,767	115,409	110,222	69,349
$\bar{N}_i$	13,308	27,764	91,343	126,729	97,772	116,369	109,577	74,595
SE	1,120	2,120	6,833	10,086	6,834	7,340	8,053	16,469
% Bias	-9.9	-3.9	-2.4	0.4	2.1	0.8	-0.6	7.6
$\underline{p}_{ci}$	0.070	0.073	0.030	0.022	0.029	0.023	0.022	0.015
$\bar{p}_{ci}$	0.079	0.076	0.030	0.022	0.029	0.023	0.023	0.015
SD	0.007	0.006	0.002	0.002	0.002	0.002	0.002	0.003
% Bias	11.8	4.6	3.0	0.2	-1.5	-0.4	1.1	-3.2
$\underline{p}_{rj}$	0.140	0.094	0.064	0.058	0.074	0.085	0.059	0.026
$\bar{p}_{rj}$	0.142	0.094	0.064	0.058	0.074	0.085	0.059	0.026
SD	0.013	0.008	0.005	0.005	0.005	0.005	0.004	0.005
% Bias	0.9	0.3	0.1	0.5	-0.1	0.3	0.2	-0.3
Total	N = 654,269 $\bar{N}_i$ = 657,458 SE = 24,407 % Bias = 0.5							

Table 16.— Results of the third Monte Carlo simulation of the fall chum salmon migrating past the marking and recapture sites on the Yukon River, Alaska, August 1 to September 24, 1996. In this simulation, fish were tagged at the marking site during the last six days of each statistical week. N_i, N, p_{ci}, p_{rj} are modeled values of the population estimates and capture probabilities. $\bar{N}_i$, $\bar{p}_{ci}$, $\bar{p}_{rj}$ are based on 500 bootstrap estimates.

	Statistical week							
	1	2	3	4	5	6	7	8
N_i	14,763	28,889	93,604	126,266	95,767	115,409	110,222	69,349
$\bar{N}_i$	15,462	29,583	94,485	127,294	95,658	115,614	111,520	69,909
SE	1,417	2,362	7,910	10,461	6,984	7,661	9,555	15,111
% Bias	4.7	2.4	0.9	0.8	-0.1	0.2	1.2	0.8
p_{ci}	0.070	0.073	0.030	0.022	0.029	0.023	0.022	0.015
$\bar{p}_{ci}$	0.068	0.072	0.030	0.022	0.030	0.023	0.022	0.015
SD	0.007	0.006	0.003	0.002	0.002	0.002	0.002	0.003
% Bias	-3.7	-1.8	-0.3	-0.1	0.5	0.3	-0.5	0.5
p_{rj}	0.140	0.094	0.064	0.058	0.074	0.085	0.059	0.026
$\bar{p}_{rj}$	0.141	0.095	0.064	0.058	0.074	0.085	0.059	0.026
SD	0.016	0.010	0.005	0.005	0.005	0.006	0.005	0.005
% Bias	0.5	1.1	0.0	0.0	-0.2	-0.1	0.2	-0.8
Total	N = 654,269 $\bar{N}_i$ = 659,525 SE = 22,045 % Bias = 0.8							

Table 17.— Results of the fourth Monte Carlo simulation of the fall chum salmon migrating past the marking and recapture sites on the Yukon River, Alaska, August 1 to September 24, 1996. In this simulation, fish were tagged at the marking site during the first six days of each statistical week and unmarked fish traveled between the marking and recapture sites in 1 day. N_i, N, p_{ci}, p_{rj} are modeled values of the population estimates and capture probabilities. $\bar{N}_i$, $\bar{p}_{ci}$, $\bar{p}_{rj}$ are based on 500 bootstrap estimates.

	Statistical week							
	1	2	3	4	5	6	7	8
N_i	14,763	28,889	93,604	126,266	95,767	115,409	110,222	69,349
$\bar{N}_i$	13,429	27,697	90,910	127,302	97,821	117,064	109,582	73,703
SE	1,053	1,979	6,985	10,098	6,844	7,313	9,226	15,987
% Bias	-9.0	-4.1	-2.9	0.8	2.1	1.4	-0.6	6.3
$\underline{p}_{ci}$	0.070	0.073	0.030	0.022	0.029	0.023	0.022	0.015
$\bar{p}_{ci}$	0.078	0.077	0.031	0.022	0.029	0.023	0.023	0.015
SD	0.006	0.006	0.002	0.002	0.002	0.001	0.002	0.003
%Bias	10.5	5.0	3.5	-0.2	-1.6	-1.0	1.3	-1.9
$\underline{P}_{rj}$	0.140	0.094	0.064	0.058	0.074	0.085	0.059	0.026
$\bar{P}_{rj}$	0.141	0.094	0.064	0.058	0.074	0.085	0.059	0.026
SD	0.013	0.008	0.005	0.005	0.005	0.005	0.005	0.005
%Bias	0.3	0.4	0.6	0.2	0.0	-0.3	0.6	0.7
Total	N = 654,269 $\hat{N}_i$ = 657,508 SE = 23,865 % Bias = 0.5							

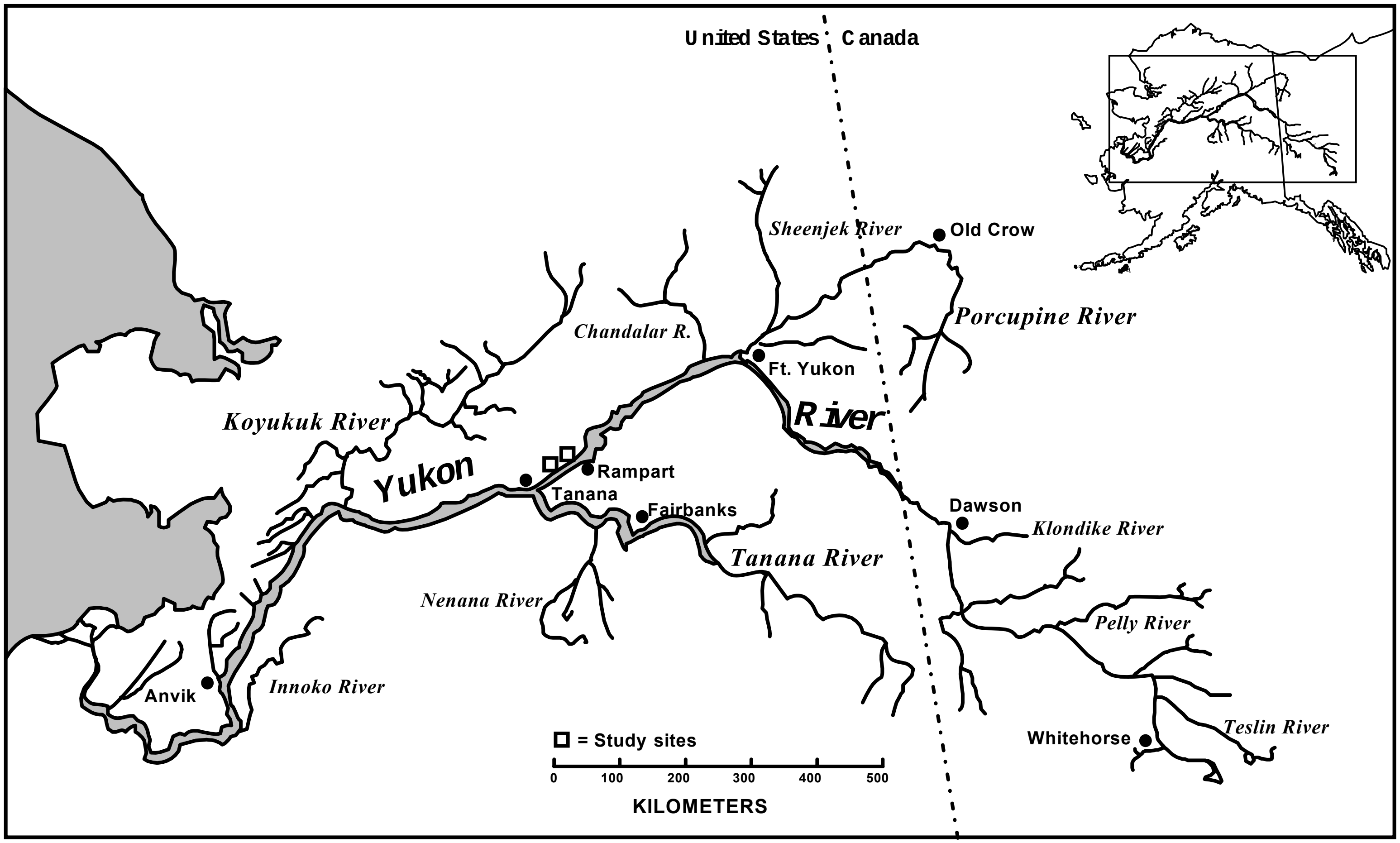

Figure 1.— Yukon River drainage showing project study sites. Open squares indicate study site locations.

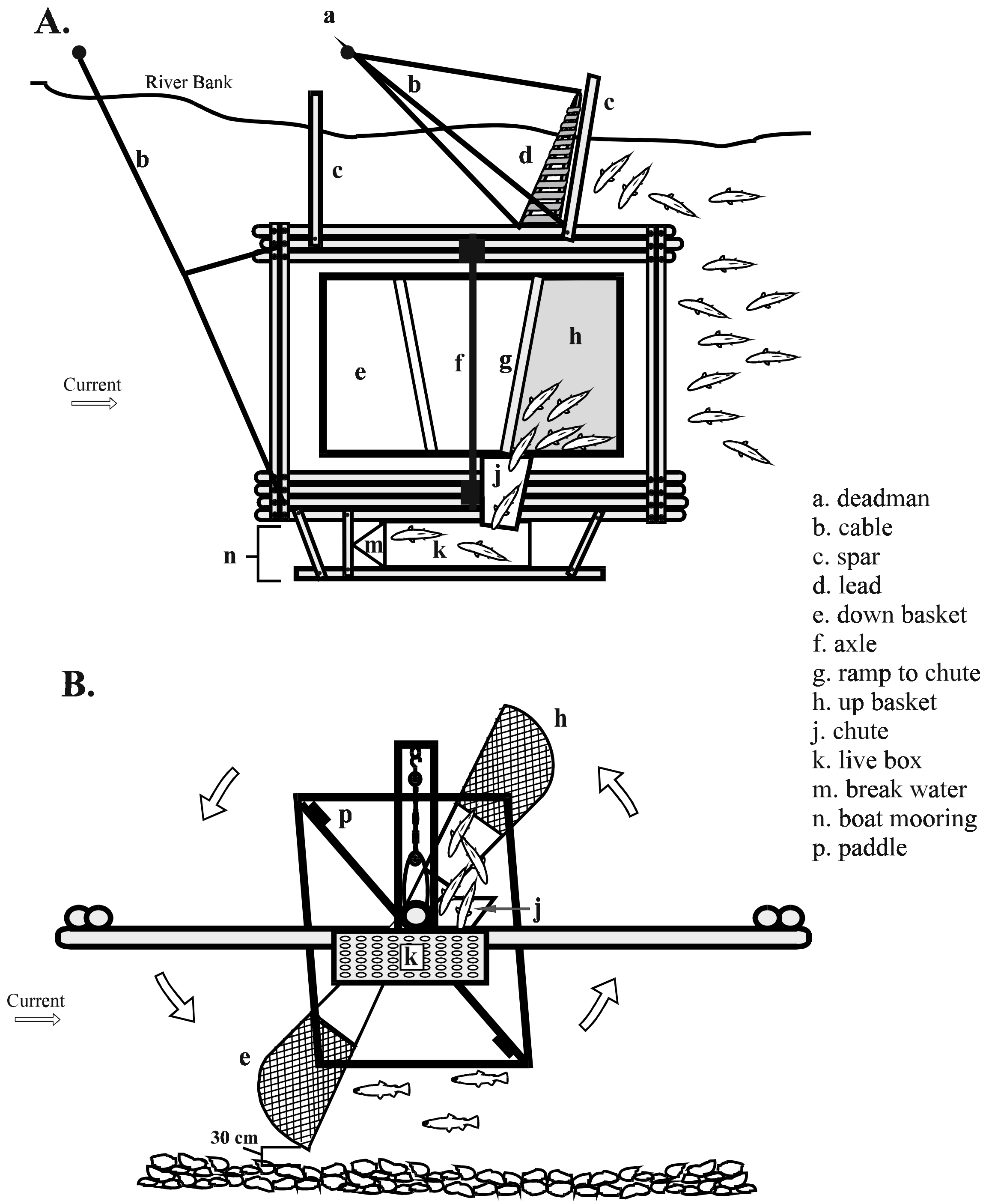

Figure 2.— Two-basket fish wheel, equipped with padded chute and live holding box, used to collect fish during the marking and recapture events. A. Aerial view. B. Side view with arrows indicating the direction of wheel movement in response to the current.

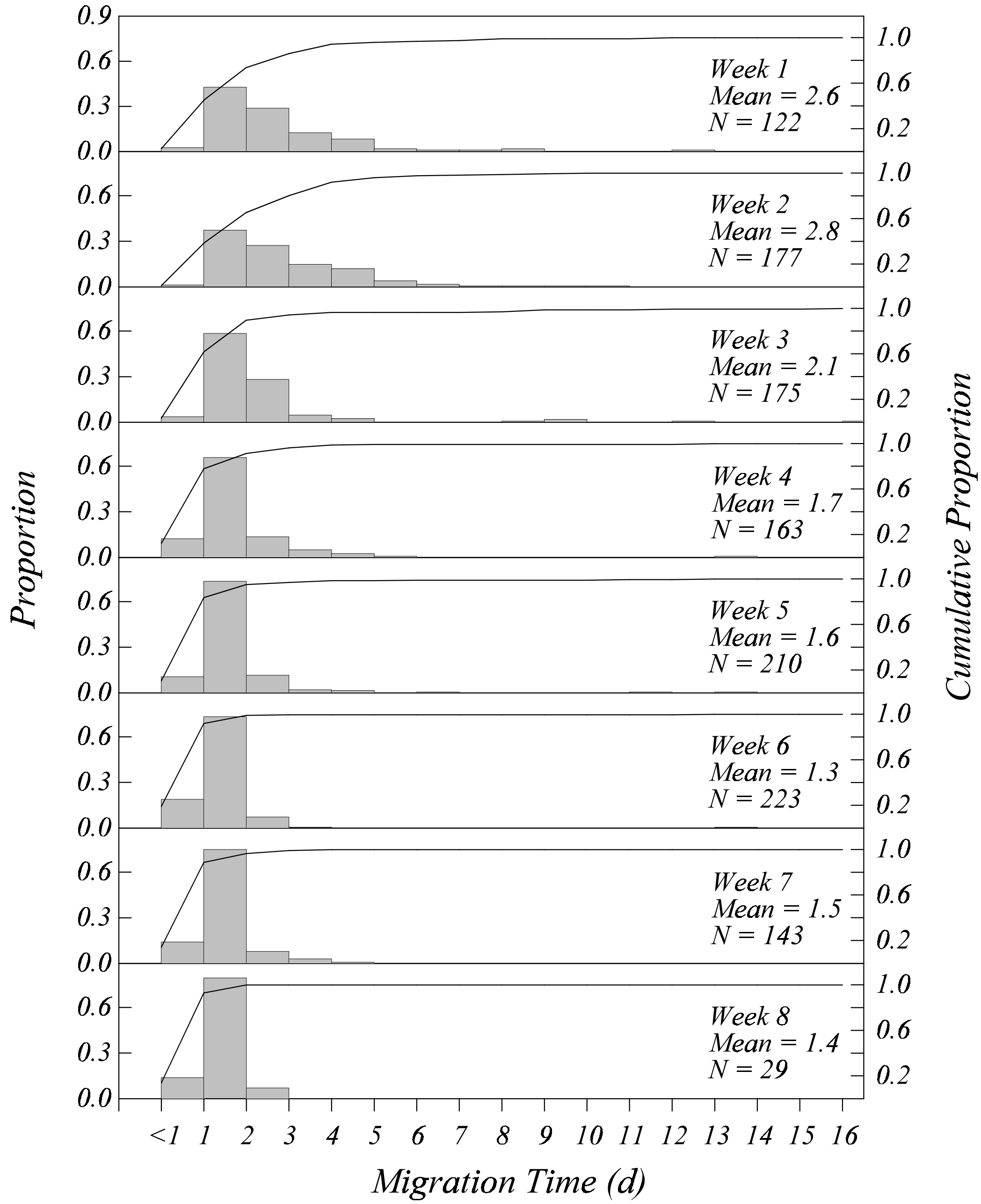

Figure 3.— Estimated migration time (d) for tagged fall chum salmon between the marking and recapture sites, by statistical week, on the Yukon River, Alaska, August 1 to September 24, 1996. Histograms represent proportion of recaptured fish. Solid lines represent cumulative proportion of recaptured fish.