North American Journal of Fisheries Management 27:860–872, 2007

DOI: 10.1577/M05-204.1

[Article]

Residual Effects from Fish Wheel Capture and Handling of Yukon River Fall Chum Salmon

JEFFREY F. BROMAGHIN
U.S. Fish and Wildlife Service, Fisheries and Ecological Services, 1011 East Tudor Road, Anchorage, Alaska 99503, USA

TEVIS J. UNDERWOOD
U.S. Fish and Wildlife Service, Arctic National Wildlife Refuge, 101 12th Avenue, Room 236, Fairbanks, Alaska 99701, USA

RAYMOND F. HANDER
U.S. Fish and Wildlife Service, Fairbanks Fish and Wildlife Field Office, 101 12th Avenue, Room 110, Fairbanks, Alaska 99701, USA

Abstract.—Since 1996, U.S. Fish and Wildlife Service biologists have annually used fish wheels to capture migrating adult fall chum salmon *Oncorhynchus keta* in the main-stem Yukon River, Alaska, and estimated their abundance via mark–recapture methods. In each year of the study, the mark rate of captured fish at a site near Rampart has been substantially greater than rates observed at numerous locations upriver of that site. The factors most likely to cause the observed reduction in the mark rate are violations of mark–recapture model assumptions or the mortality of marked fish between the Rampart site and upriver locations. Results of studies conducted through 2000 were most consistent with the hypothesis of mortality. We investigate potential explanatory factors for the apparent reduction in mark rates at upriver locations using data collected during additional studies from 2001 to 2003. Results document that holding fish in submerged pens at the marking site negatively affects their ability to migrate for at least some time. No evidence of tag loss or spatial segregation within the mark–recapture study area was observed. A conclusion that some aspect of the capture and handling of fish elevates their mortality upriver of the mark–recapture study area seems well founded. However, holding of fish does not solely explain the reduction in mark rates at upriver locations, and other contributing factors remain unidentified. Researchers using fish wheels should be aware that the gear may be more harmful to fish than was previously thought and may bias estimators of some parameters such as abundance or migration speed.

In 1996, the U.S. Fish and Wildlife Service (USFWS) initiated an annual mark–recapture study to estimate the abundance of migrating adult fall chum salmon *Oncorhynchus keta* on the Yukon River main stem above the Tanana River confluence near Rampart, Alaska (Underwood et al. 2004 and 2007). Biologists associated with the study became aware that mark rates (i.e., the proportion of a catch that has been marked) of fish captured near Rampart were substantially greater than those at distant locations upriver of that site. Underwood et al. (2004) constructed a list of potential causes of the reduced mark rates, including tag loss, gear avoidance, and selective harvest and evaluated the plausibility of each potential cause using available information. They found that mark rates tended to decline as distance from the marking site increased. They also found that the number of times a chum salmon was captured in a fish wheel was inversely related to the probability of recapture at locations upriver from the mark–recapture study area. Although the data were not conclusive, Underwood et al. (2004) reasoned that an elevated mortality rate of marked fish upriver from the study area appeared most consistent with the available information.

We are not aware of any investigations that have documented elevated mortality rates in fish wheel mark–recapture studies of migrating adult chum salmon. However, Cleary (2003) found that fish wheel capture and tagging of migrating adult fall chum salmon in the Tanana River had metabolic consequences. In addition, numerous studies have documented stress, a behavioral response, or mortality associated with the capture and handling of salmonids and related species (e.g., Bernard et al. 1999; Buchanan et al. 2002; Budy et al. 2002; Clements et al. 2002).

The National Marine Fisheries Service (NMFS) conducted a telemetry study of fall chum salmon in 1998 and 1999 in conjunction with the Rampart mark–recapture study. Results of that study may provide

* Corresponding author: jeffrey_bromaghin@fws.gov

Received November 15, 2005; accepted October 20, 2006
Published online July 26, 2007

information on handling effects and potential upriver mortality (results currently unpublished; John Eiler, NMFS Auke Bay Laboratory, Juneau, Alaska, personal communication). The potential fall chum salmon mortality increase caused by the mark–recapture study within the Yukon River drainage is cause for concern. Annual chum salmon catches have exceeded 18,000 at the marking site and 40,000 at the recapture site, and weekly estimates of capture probability have exceeded 0.10 at the marking site and 0.15 at the recapture site. If fish captured during the course of the study have an elevated mortality rate, a substantial number of fish and a substantial proportion of the population could be affected. Important fisheries, particularly subsistence (USA) and First Nation (Canada) fisheries, occur in upper portions of the drainage, and it would be difficult to justify an investigation that substantially elevated mortality, particularly in years of low abundance when fisheries are restricted or closed. This possibility, in combination with a weak fall chum salmon return, led to the early termination of the study in 2000.

The potential for fish wheels to negatively affect fish has ramifications beyond the Yukon River drainage. Fish wheels are commonly used in Alaska to provide data for in-season management of salmon fisheries and are a method of capture in research programs (e.g., Meehan 1961; Merritt and Roberson 1986; Cappiello and Bromaghin 1997; Johnson et al. 2002; Savereide 2003; Stuby 2003). They are also used in other locations on the West Coast of North America (e.g., Link and Peterman 1998; Link and English 2000). One reason that use of fish wheels has increased within Alaska is that they are efficient under suitable conditions and are assumed to provide a relatively harmless method of capturing fish. A finding that fish wheel capture or subsequent handling is harmful to fish could have important consequences for numerous management and research programs.

Additional investigations of various aspects of the reduced mark rates were conducted from 2001 to 2003. One objective was to further test the equality of mark rates at upriver locations. Some mark rate estimates from the Yukon River main stem reported by Underwood et al. (2004) were obtained during a limited portion of the migration, and two tributaries with abundant populations had only been sampled in one prior year. Additional objectives included testing hypotheses that (1) the probability of recapture and travel time between locations were independent of fish handling practices and (2) tag loss within the Yukon River main stem did not occur. Finally, we tested mark–recapture model assumptions regarding fish behavior within the mark–recapture study area, namely interrelated aspects of mixing and spatial segregation.

Methods

Study area.—The Yukon River originates in the coastal mountains of northern British Columbia; flows over 3,200 km through British Columbia, the Yukon Territory, and Alaska; and empties into the eastern Bering Sea. It is the fourth largest drainage in North America, draining an area of approximately 860,000 km^2, and has a mean annual discharge of nearly 5,700 m^3/s (Brabets et al. 2000). Fall chum salmon tend to enter the Yukon River from midsummer through early fall and spawn in areas of upwelling groundwater in the upper portions of the drainage. Important fall chum salmon spawning areas include portions of the Tanana, Chandalar, and Porcupine rivers and the Yukon River main stem and its tributaries in Canada (Figure 1).

Rampart mark–recapture study.—The foundation of this investigation is the Rampart mark–recapture study conducted annually from 1996 to 2005 (Underwood et al., 2007). The study was implemented as a temporally stratified, two-event, mark–recapture study, using the estimator of Darroch (1961) to provide weekly and seasonal estimates of fall chum salmon abundance. Fish wheels were used to capture fish at the marking and recapture sites (Figure 1). Several modifications to fish wheel construction were made to reduce capture-induced injury to fish. Fish processing consisted of determining gender from an examination of external morphology, measuring length from mid-eye to tail fork (cm), applying an individually numbered spaghetti tag, and clipping a fin as a secondary mark.

At the marking site, fish were captured in two fish wheels located on opposite banks of the river (Figure 1) and were processed during four daily tagging sessions to spread the release of tagged fish throughout the day. During a single session, fish captured at the first fish wheel operated by the crew were obtained from the chute, processed, and placed into a live-box. Unmarked fish that fell into the live-box were enumerated and their capture times were recorded, which allowed the calculation of a measure of crowding in the live-box. At the approximate midpoint of the tagging session, or when half of the target number of fish for the session had been tagged, the crew proceeded to the second fish wheel, where all fish were captured from the chute, processed, and released immediately. At the end of the tagging session, the crew revisited the first fish wheel and simultaneously released all fish being held. The times of fish capture and release were recorded to the nearest minute. The first fish wheel visited was alternated between tagging sessions within a day and between the first sessions of consecutive days in an attempt to avoid potential bias caused by any differences between banks of the river or

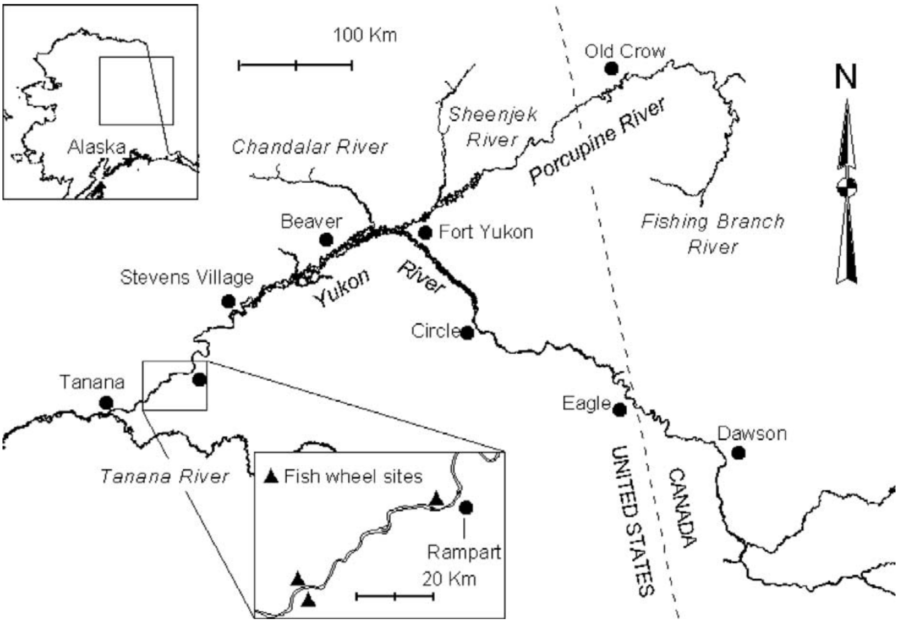

FIGURE 1.—Map of the fall chum salmon mark–recapture study area within the upper Yukon River drainage, Alaska and Canada (originally from Underwood et al. 2004).

fish wheels. In 2002, fish being held during the first tagging session of each day were not released until the beginning of the second session to increase the holding time of some fish. No fish were held in 2003.

A single fish wheel was used at the recapture site near Rampart (Figure 1). The fish wheel was operated 24 h/d, 7 d/week, except for occasional brief periods when maintenance was required. Each captured fish was examined for the presence of primary and secondary marks and released. When possible, the crew used dip nets to capture fish directly from the chute. Otherwise, fish passed down the chute into the live-box and were subsequently removed by dip net. The numbers of tagged and untagged fish caught, the tag numbers of tagged fish, and any incidence of tag loss were recorded. In 2002, operational plans called for digital photographs to be taken of the first 15 fish captured each day to document the physical condition of marks and any occurrence of tag loss. In 2003, a video system was installed that allowed discontinuation of live-box recapture at the Rampart site (Daum 2005).

Upriver fish wheel operations.—In 2001, additional recapture fish wheels were operated near Beaver and Circle (Figure 1) to obtain improved estimates of mark rates at upriver locations. Operational plans called for these fish wheels to sample for a minimum of 6 h/d on 5 d/week. The fish wheel contractors were to keep the fish wheels operating efficiently and monitor them while in use. The date and time of fish wheel operations, the total number of fish captured, the number of tagged fish captured, and any incidence of tag loss were recorded. Two fish wheels used to mark fish in an independent mark–recapture experiment conducted by the Canada Department of Fisheries and Oceans (DFO) also served as recapture fish wheels for the Rampart study; these fish wheels were located approximately 8 km apart on the right bank of the Yukon River main stem in Canada near the U.S. border (Figure 1). These fish wheels operated 24 h/d, 7 d/week, except during brief servicing periods. Fish were captured and held in live-boxes from which they were removed, tagged, and released during three daily tagging sessions (Pat Milligan, Canada DFO, Whitehorse, Yukon, personal communication).

In 2002, in addition to the fish wheels used in 2001, a fish wheel was operated near Stevens Village, Alaska (Figure 1). Fishing effort varied among the recapture fish wheels. Operational plans called for 6-h/d, 7-d/week operation at Stevens Village; 10-h/d, 5-d/week operation at Beaver; and 6-h/d, 5-d/week operation at Circle. The fish wheel contractors were to keep the fish wheels operating efficiently and monitor them during sampling. The date and time of fish wheel operations, the total number of fish captured, the number of tagged fish recaptured, and any incidence of tag loss were recorded. Digital photographs were to be taken of the first 15 fish captured each day to document the physical condition of the marks and any occurrence of tag loss. The two Canada DFO fish wheels were operated near the international border as in 2001. Because the focus of the investigation shifted in 2003, fish wheel operations at Stevens Village, Beaver, and Circle were not conducted in that year.

Tributary sampling in 2003.—Sampling was conducted within the Chandalar and Sheenjek rivers to estimate the proportions of fall chum salmon that had been marked. Both rivers support large spawning populations, but they had only been sampled in one prior year (Underwood et al. 2004). Early (access by boat) and late (access by helicopter) season sampling trips to spawning areas were scheduled using available run timing information. Aerial surveys were conducted along the river corridor at 90–240 m above ground level until a concentration of carcasses was encountered. Sampling was conducted in areas with the greatest density of carcasses to maximize sampling efficiency.

Sampling was conducted along the shoreline and in water depths that could be waded, and a telescoping barbed gig was used to access carcasses for examination. Each fish sampled was examined for the presence of both primary and secondary marks. A fish with no spaghetti tag and no adipose fin was further examined for the presence of a tagging wound. The number of marked fish was recorded, excluding fish for which tagging status could not be determined with confidence.

Gill-net sampling in 2003.—In 2003, gill nets were drifted offshore of the Rampart fish wheel to investigate the possibility of spatial segregation or a lack of mixing within the mark–recapture study area. Drift gill nets were fished during three 5-d periods corresponding to the early, middle, and late portions of the fall chum salmon migration: 7–11 August, 25–29 August, and 9–13 September. Gill nets were 45.7 m long; were 5.5, 6.7, or 7.9 m deep; and had 14.4-cm stretch-mesh netting (15 Momoi MMT).

Gill nets were drifted in waters offshore of and adjacent to the fish wheel. Markers were placed on the shore approximately 0.5 km upriver and downriver of the fish wheel to designate the starting and stopping points of drifts so that the fish wheel was passed at the approximate midpoint of each drift. Starting and stopping times were recorded for each drift. Each fish captured was examined for the presence of primary and secondary marks.

The clocks used for recording gill-net deployment times were synchronized with the internal computer clock of the video system used to place a time and date stamp on video images at the recapture fish wheel. The time data were used to identify the subset of the video images that were stored during each gill-net drift, allowing gill-net and fish wheel catches to be closely matched in time. The number of marked fish and the total number of fish captured during each gill-net drift and in the fish wheel during the corresponding period of time were enumerated.

Data analysis.—In 2001 and 2002, holding time (h) at the marking site was computed as the time between capture and release. For each fish held in a live-box, the number of other fish simultaneously present in the live-box was determined. A measure of crowding for each fish was computed as the summed overlap in holding time with that of all other fish sharing time in the live-box. Travel time between two sites was computed as the time between the last release at the downriver site and the first capture at the upriver site. Travel time between the marking site and the Rampart recapture site was recorded to the nearest minute, whereas all other travel times were recorded to the nearest day. The number of times individual fish were captured at each location was also determined. In all analyses, gender was coded as an indicator variable: 1 denoted a female and 0 denoted a male.

The probability of recapture at upriver locations and the travel time to these locations were modeled using generalized linear models (Agresti 2002). The probability of recapture was modeled as a binomial random variable with a logit link, whereas travel time was modeled as an inverse Gaussian random variable (Johnson et al. 1995; Zabel et al. 1998) with an identity link. Explanatory variables considered for inclusion in the models were fish gender and length, holding time at the marking site, crowding at the marking site, and the number of times a fish was captured at each downriver location. Weekly strata (defined at the marking site for temporally stratified abundance estimation) were utilized as categorical nuisance parameters to adjust for possible temporal changes in such factors as water velocity or fish wheel efficiency, essentially including a base recapture rate or travel time for fish released in each marking stratum. The parameters of all generalized linear models were estimated using the GENMOD procedure in the Statistical Analysis System STAT software version 8.02 (SAS Institute 1999).

The analysis of each response variable began by fitting a model that included all explanatory variables and all possible interactions, termed the full model. If the parameters of the full model were not estimable, the highest-order interactions that could not be estimated were sequentially eliminated from the model until the remaining parameters were estimable. Likelihood ratio tests (Stuart et al. 1999) were used to develop the most parsimonious model possible for each response variable. Terms were eliminated in stepwise fashion, beginning with the highest-order interaction and ending with main effects, until all remaining terms were either statistically significant or nested within other terms that were statistically significant. When considering terms of the same order of interaction for exclusion from the model (e.g., among all three-way interactions), the least significant term was eliminated first. A significance level of 0.025 was used during model development.

A test of bank-to-bank mixing of marked fish between the marking site and the Rampart site is conducted annually as a routine component of the mark–recapture data analysis (Underwood et al., 2007). Additional insight into mixing can be obtained from knowledge of the bank of tagging for fish recaptured upriver. Such an analysis, for example, could reveal that certain populations prefer one bank to the other at the marking site, which could cause differential mark rates among populations. Of all fish tagged during mark–recapture operations, the proportion captured in the right-bank fish wheel was computed. For each recapture location, the bank at which each recaptured fish was tagged was determined. The hypothesis that the proportion of recaptured fish tagged at the right-bank fish wheel was equal to the proportion of all tagged fish originating from the right-bank fish wheel was tested using an exact binomial test (Hollander and Wolfe 1999; Agresti 2002). A separate, identical hypothesis was tested for each main-stem recapture location. Fish that escaped before their tag number (and therefore bank of tagging) could be determined were excluded from the analysis.

Mark rates reported by Underwood et al. (2004) consistently decreased as the distance from the marking site increased. If the decline was solely attributable to the effects of holding fall chum salmon in a live-box, the proportion of a catch composed of marked fish that were not held should be equal among all recapture sites. To investigate this possibility, recaptured fish were classified according to whether or not they had been held, and the proportion of the catch in each category was computed. Generalized linear models (Agresti 2002) of the proportions that were and were not held were fit to the data using a logit link and a binomial error distribution, using distance from the marking site as an explanatory variable. Likelihood ratio tests and chi-square test statistics (χ^2; Stuart et al. 1999) were used to test hypotheses that model parameters were equal for fish that were and were not held and that the distance coefficient was zero for fish that were not held.

The hypothesis that mark rates of fish susceptible to capture in the offshore gill nets and fish wheels in 2003 were equal was tested using an exact Cochran–Mantel–Haenszel (CMH) test (Agresti 2002), as implemented in StatXact version 6.1 (Cytel 2003). The test allows mark rates to vary between levels of a stratification variable but is sensitive to consistent patterns between the experimental variables—in this case, capture method and tag status. The three periods of data collection formed a three-level stratification variable for this test. Monte Carlo methods (Manly 1991) with 100,000 replications were used to estimate the significance of the test.

The equality of mark rates at recapture locations in 2003 was evaluated using exact binomial tests implemented in StatXact (Cytel 2003). A likelihood ratio test statistic (Agresti 2002) was used for each test, and significance was estimated using Monte Carlo methods (Manly 1991) with 100,000 replications. Mark rates were compared among the four upriver locations, as well as between Rampart and the upriver locations.

Results

Catch Statistics

Fish wheels at the marking site operated from 30 July to 15 September in 2001, releasing 8,490 marked fall chum salmon. Of these, 48.1% were released from the right-bank fish wheel and 70.7% were held in a live-box. Fish that were held had an average holding time of 1.0 h and an average crowding measure of 26.4 fish-hours. In 2002, 5,518 marked fish were released from 29 July to 14 September. Of these, 42.7% were released from the right bank and 52.3% were held. The fish that were held had an average holding time of 2.7 h and an average crowding of 87.6 fish-hours.

Catches at the Rampart fish wheel totaled 11,814 in 2001 and 14,478 in 2002, whereas catches at upriver recapture locations were much lower, ranging from 559 to 5,578 fish (Table 1). Mark rates among fish wheels ranged from 1.56% to 4.24% in 2001 and from 1.42% to 4.58% in 2002. In 2001, the mark rate observed at the Rampart fish wheel was substantially greater than that observed at any of the upriver locations. In 2002, the mark rates observed at the Circle and Canada DFO fish wheel locations were again much lower than that at Rampart, although the Stevens Village and Beaver mark rates were equal to or exceeded that observed at Rampart. One peculiarity of the Stevens Village fish wheel data collected in 2002 is that approximately half of the recaptured fish were caught over a 4-d period; the high mark rate may therefore be an anomaly. In 2002, the Beaver fish wheel caught very few fish before 5 September, the approximate midpoint of the migration, so at that time the fish wheel was moved to a new location that proved to be more productive.

In 2002, we obtained 481 digital photographs of

TABLE 1.—Catch statistics for adult fall chum salmon marked with spaghetti tags at two fish wheels in the Yukon River near Tanana, Alaska, and recaptured at five upriver fish wheel locations (Figure 1; ND = no data were collected; Canada = two fish wheels operated by Canada DFO near the U.S. border).

Recapture location	First date	Last date	Recaptures		Proportion marked	95% confidence limits	
			Marked	Total		Lower	Upper
2001							
Rampart	31 Jul	15 Sep	501	11,814	0.0424	0.0388	0.0460
Stevens Village	ND	ND	ND	ND	ND	ND	ND
Beaver	12 Aug	26 Sep	19	807	0.0235	0.0131	0.0340
Circle	13 Aug	29 Sep	42	2,387	0.0176	0.0123	0.0229
Canada	2 Aug	4 Oct	51	3,277	0.0156	0.0113	0.0198
2002							
Rampart	30 Jul	18 Sep	434	14,478	0.0300	0.0272	0.0328
Stevens Village	22 Aug	25 Sep	66	1,441	0.0458	0.0350	0.0566
Beaver	8 Aug	25 Sep	17	559	0.0304	0.0162	0.0447
Circle	16 Aug	1 Oct	14	902	0.0155	0.0074	0.0236
Canada	26 Jul	7 Oct	79	5,578	0.0142	0.0111	0.0173

chum salmon from the Rampart recapture site, 401 from Stevens Village, 221 from Beaver, and 252 from Circle. We found no incidence of tag loss, and both primary and secondary marks were clearly distinguishable.

Recapture Probability Models

Fish held in a live-box at the marking site had a greater probability of recapture at Rampart than did immediately released fish in both 2001 and 2002. The model for 2001 contained an intercept for each marking stratum and a term for holding time (Table 2). The estimated parameter for holding time was significantly greater than zero, indicating that increased holding time was associated with an increased probability of recapture. Similar results were obtained with 2002 data. The final model for 2002 contained an intercept term for each stratum at the marking site, a term for fish gender, and a term for holding time. As in 2001, the probability of capture was positively related to holding time in 2002 (Table 3). In addition, males had a greater recapture probability than did females in 2002.

The increased recapture probability at Rampart caused by holding fish will positively bias mark rate estimates and negatively bias abundance estimates. Unfortunately, given individual holding times, variation in individual fish responses from the model, and the confounding between capture probability and travel time parameters (Darroch 1961), it is difficult to precisely correct for the bias in the Rampart mark rate and abundance estimates. However, a general sense of the magnitude of the biases can be obtained using the proportion of fish that were held, the mean holding time, and estimated model parameters. Using the parameter estimates to compute the probability of recapture for fish that were not held and for fish that were held for the mean holding time, suggests that

TABLE 2.—Parameter estimates and inferential statistics for a generalized linear model of the probability that an adult fall chum salmon marked with a spaghetti tag at two fish wheels in the Yukon River near Tanana, Alaska, would be recaptured upriver in a fish wheel near Rampart in 2001. Holding time indicates the duration for which fish were held in live-boxes at the marking site.

Parameter	Estimate[a]	SE	χ^2
Intercept–stratum 1	−2.8014	0.1636	293.2
Intercept–stratum 2	−2.6469	0.0956	766.9
Intercept–stratum 3	−2.6730	0.1054	643.6
Intercept–stratum 4	−2.9536	0.1119	696.4
Intercept–stratum 5	−3.5933	0.1669	463.3
Intercept–stratum 6	−3.6333	0.2054	312.9
Intercept–stratum 7	−4.6149	0.3751	151.3
Holding time (h)	0.3634	0.0751	23.4

[a] For all parameters, df = 1 and $P < 0.0001$.

TABLE 3.—Parameter estimates and inferential statistics for a generalized linear model of the probability that an adult fall chum salmon marked with a spaghetti tag at two fish wheels in the Yukon River near Tanana, Alaska, would be recaptured upriver in a fish wheel near Rampart in 2002. Holding time indicates the duration for which fish were held in live-boxes at the marking site.

Parameter	Estimate[a]	SE	χ^2	P
Intercept–stratum 1	−3.2858	0.3460	90.2	<0.0001
Intercept–stratum 2	−2.9709	0.2918	103.6	<0.0001
Intercept–stratum 3	−3.1181	0.2455	161.3	<0.0001
Intercept–stratum 4	−2.6004	0.1405	342.5	<0.0001
Intercept–stratum 5	−2.3495	0.1160	410.0	<0.0001
Intercept–stratum 6	−2.4448	0.1160	444.1	<0.0001
Intercept–stratum 7	−2.3177	0.1360	290.4	<0.0001
Gender (female = 1)	−0.2281	0.1013	5.1	0.0243
Holding time (h)	0.1031	0.0272	14.3	<0.0001

[a] For all parameters, df = 1.

TABLE 4.—Parameter estimates and inferential statistics for a generalized linear model of the probability that an adult fall chum salmon marked with a spaghetti tag at the two fish wheels in the Yukon River near Tanana, Alaska, would be recaptured at one of three upriver fish wheel sites (Beaver, Circle, and Canada DFO; Figure 1) in 2001. Holding time indicates the duration for which fish were held in live-boxes at the marking site.

Parameter	Estimate[a]	SE	χ^2	*P*
Intercept	−4.0298	0.1198	1,130.7	<0.0001
Holding time (h)	−0.5197	0.1541	11.4	0.0007

[a] For both parameters, df = 1.

Rampart mark rate estimates were positively biased by approximately 23.6% in 2001 and 15.5% in 2002. Mark rate biases of this magnitude would negatively bias corresponding abundance estimates by approximately 19.1% and 13.4%. These bias statistics should be viewed as approximations for the reasons stated.

Holding fish in a live-box appeared to significantly decrease their probability of recapture at the upriver recapture locations in 2001, but a significant relationship was not apparent in 2002. In 2001, relatively few fall chum salmon were recaptured at the Beaver, Circle, and Canada DFO fish wheels, so modeling the probability of recapture at individual locations was not attempted. Data from the three locations were pooled and treated as if they had originated from a single location. Because of the small number of recaptures, even in the pooled data set, models with high-order interactions failed to converge. For that reason, model building began with a model containing an intercept term for each marking stratum, terms for fish gender, fish length, holding time, the measure of crowding, the number of times fish were captured at the marking site, the number of times fish were captured at Rampart, and all two-way interactions. After insignificant terms were eliminated, the final model contained a single intercept term and a term for holding time (Table 4). The holding time parameter was significantly less than zero, reflecting the finding that holding time was inversely related to the probability of recapture in the upriver fish wheels. Final models of the probability of recapture in the upriver fish wheels in 2002 did not contain terms for either holding time or the measure of crowding and therefore are not presented.

Travel Time Models

Fish held in a live-box traveled more slowly between the marking site and the Rampart recapture site than fish that were not held. Models of travel time between the marking site and Rampart contained different explanatory variables in 2001 and 2002, but both models suggested that holding fish in a live-box was associated with an increased travel time. A significant interaction between two variables (holding time and the number of times a fish was captured at the marking site) was encountered during the analysis of the 2001 data ($P = 0.0019$). The model indicated that the travel time of fish caught once increased with holding time but that the opposite relationship existed for fish caught more than once. We attempted to verify the practical significance of the interaction by comparing plots of the model and the data. No explanation for the difference was apparent, relatively few fish were caught more than once, and the interaction term primarily modified the model in a region of extremely low data density. For those reasons, the interaction was judged to be spurious, and model development proceeded as if the term had not been significant. The final model for the 2001 data contained an intercept for each marking stratum and terms for fish gender, length, and holding time (Table 5). The estimated holding time parameter was positive, indicating that increased holding time was associated with increased travel time to Rampart.

TABLE 5.—Parameter estimates and inferential statistics for a generalized linear model of travel time (d) for spaghetti-tagged adult fall chum salmon between the Yukon River marking site (two fish wheels near Tanana, Alaska) and the recapture site (fish wheel near Rampart) in 2001. Holding time indicates the duration for which fish were held in live-boxes at the marking site.

Parameter	Estimate[a]	SE	χ^2	*P*
Intercept–stratum 1	−0.1441	1.1533	0.0	0.9006
Intercept–stratum 2	−1.0039	1.0851	0.9	0.3549
Intercept–stratum 3	−0.6047	1.0899	0.3	0.5790
Intercept–stratum 4	−1.0621	1.0810	1.0	0.3259
Intercept–stratum 5	−1.7707	1.0398	2.9	0.0886
Intercept–stratum 6	−1.6473	1.0422	2.5	0.1140
Intercept–stratum 7	−2.0728	1.1120	3.5	0.0623
Gender (female = 1)	0.6729	0.1175	32.8	<0.0001
Length (cm)	0.0530	0.0181	8.6	0.0035
Holding time (h)	0.2324	0.0957	5.9	0.0151

[a] For all parameters, df = 1.

In 2002, holding fish under crowded conditions increased the travel time to Rampart. The final model of travel time to Rampart contained an intercept term for each marking stratum and a term for the measure of crowding (Table 6). Although crowding and holding time were positively correlated (Pearson's product-moment correlation coefficient = 0.84), crowding provided a substantially better model of these data than did holding time.

In both 2001 and 2002, the small number of recaptures from the locations upriver of Rampart

TABLE 6.—Parameter estimates and inferential statistics for a generalized linear model of travel time (d) for spaghetti-tagged adult fall chum salmon between the Yukon River marking site (two fish wheels near Tanana, Alaska) and the recapture site (fish wheel near Rampart) in 2002. Crowding was computed for each fish as the summed overlap in holding time (h) with that of other fish held simultaneously in the live-box at the marking site.

Parameter	Estimate[a]	SE	χ^2	P
Intercept–stratum 1	2.9634	0.4862	37.2	<0.0001
Intercept–stratum 2	3.0680	0.4292	51.1	<0.0001
Intercept–stratum 3	5.1275	0.7610	45.4	<0.0001
Intercept–stratum 4	3.8455	0.2696	203.4	<0.0001
Intercept–stratum 5	2.3286	0.1019	522.3	<0.0001
Intercept–stratum 6	1.4223	0.0569	625.3	<0.0001
Intercept–stratum 7	1.3250	0.0538	607.6	<0.0001
Crowding (fish-hours)	0.0017	0.0004	14.7	0.0001

[a] For all parameters, df = 1.

precluded modeling of travel time. Because of the large distance between the locations, pooling data from the individual locations was deemed inappropriate.

Bank of Initial Tagging

Tagged fish were not strongly bank-oriented at the tagging site in either 2001 or 2002 (Figure 2). Of the 8,490 fall chum salmon tagged in 2001, 48.1% were tagged at the right-bank fish wheel. For the collection of fish recaptured at each of the four 2001 recapture sites, an exact binomial test that 48.1% of the recaptures had been tagged on the right bank was only significant for fish recaptured at Beaver (Table 7). Of the 5,518 fall chum salmon tagged in 2002, 42.7% were released from the right-bank fish wheel. None of the exact binomial tests for the 2002 recapture locations was statistically significant.

Recovery Rates

Mark rates in the 2001 and 2002 fish wheel catches generally declined with distance from the marking site, but holding fish in a live-box did not fully explain the decline (Figure 3). Given the positive bias of the Rampart mark rate estimate previously described, the number of marked fish that were recaptured at Rampart in 2001 and 2002 was reduced accordingly, as an approximate correction, before fitting the generalized linear models. Although the models for fish that were held declined more steeply with distance than the models for fish that were not held, the distance coefficients of these models within each year were not significantly different in either 2001 ($P = 0.5996$) or 2002 ($P = 0.0590$). In addition, distance coefficients for fish that were not held were significantly different than zero in both 2001 ($P < 0.0001$) and 2002 ($P = 0.0026$).

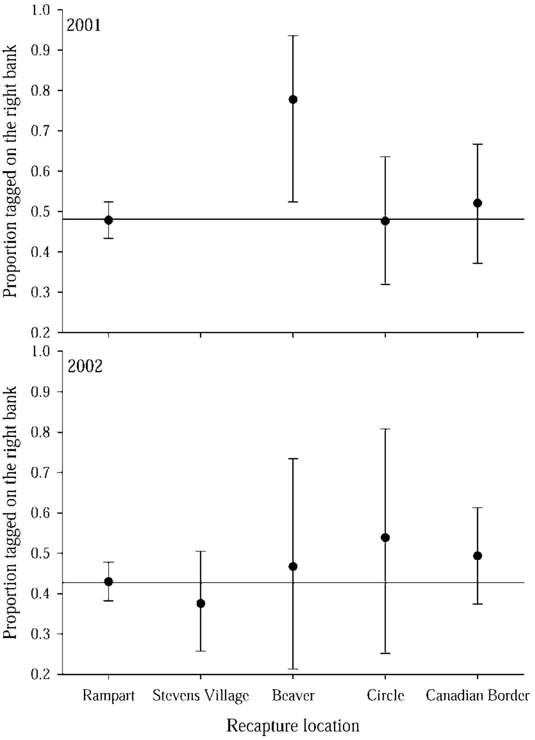

FIGURE 2.—Proportions (95% CI) of Yukon River fall chum salmon adults recaptured at five upriver fish wheel locations in 2001 and 2002 (Stevens Village was not sampled in 2001) that were marked (spaghetti tags) at the right-bank fish wheel near Tanana, Alaska. Horizontal lines represent proportions of all tagged fish that were released from the right-bank fish wheel.

No evidence of incomplete mixing or spatial segregation was detected in the paired gill-net and fish wheel data collected at Rampart in 2003. Fish wheel catches in the three sampling periods were 122, 319, and 900 fall chum salmon, whereas corresponding gill-net catches were 105, 366, and 402 fish (Table 8). The exact CMH test of mark rate equality between the two gears was not significant ($P > 0.9999$).

The mark rate estimated at Rampart was approximately double those of the pooled upriver sites in 2003 (Table 9). At Rampart, 34,769 fish were examined, 422 of which were marked. Sampling conducted in the Chandalar River from 26 August to 2 October resulted in the examination of 486 fall chum salmon carcasses, 1 of which had a secondary mark. On 10 October, an additional 3,195 fall chum salmon carcasses from the Chandalar River were examined, and 15 of those had either primary or secondary marks. An exact binomial test of equality of mark rates from the two Chandalar River samples suggested that they were not significantly different ($P = 0.5063$); the two samples were

TABLE 7.—Results of exact binomial tests of the hypothesis that the proportions of Yukon River fall chum salmon adults recaptured at five upriver fish wheel locations that were marked (spaghetti tags) at the right-bank fish wheel near Tanana, Alaska, equaled the proportion of all marked fish released from the right-bank fish wheel (Figure 1; ND = no data were collected; Canada = two fish wheels operated by Canada DFO near the U.S. border) in 2001 and 2002.

Recapture	*N*	*Z*	*P*
	2001		
Rampart	489	−0.1094	0.9493
Stevens Village	ND	ND	ND
Beaver	18	2.5201	0.0204
Circle	42	−0.0624	>0.9999
Canada	48	0.5523	0.6827
	2002		
Rampart	431	0.1022	0.9555
Stevens Village	64	−0.8378	0.4790
Beaver	15	1.1462	0.9490
Circle	13	0.8140	0.5885
Canada	73	1.1462	0.3041

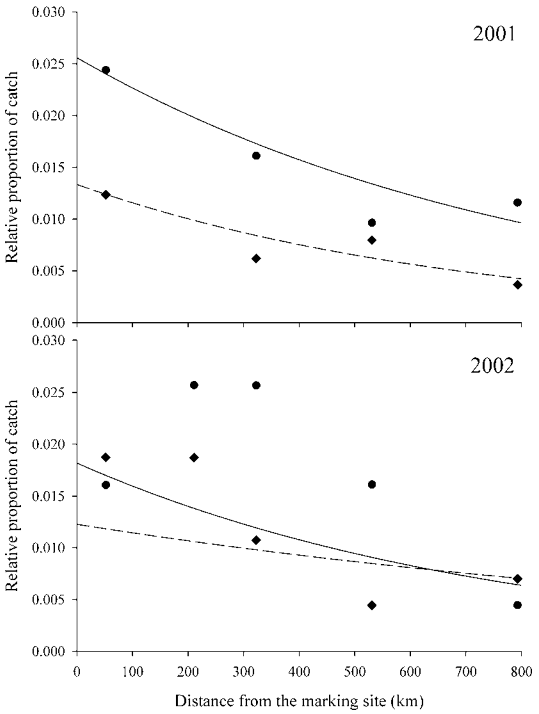

FIGURE 3.—Generalized linear models of the proportion of adult Yukon River fall chum salmon captured at upriver locations that had been marked (mark rate) in 2001 (Stevens Village was not sampled) and 2002, using river kilometers from the marking site near Tanana, Alaska, as an explanatory variable. Fish were either held in live-boxes for several hours (model = solid line, data = circles) or immediately released (model = dashed line, data = diamonds) after tagging.

therefore pooled (Table 9). Because of weather conditions, only one sampling trip was made to the Sheenjek River, during which 1 fish with a primary mark was observed among 190 fish. The crew of the Fishing Branch River weir sampled 924 fall chum salmon, 6 of which were marked. Catches in the Canada DFO fish wheels totaled 5,582, of which 39 were marked. Mark rates in the upriver samples ranged from 0.0042 in the pooled Chandalar River sample to 0.0070 in the Canada DFO sample. An exact test of equality of mark rates observed in the pooled Chandalar River sample and the other three upriver locations was not significant ($P = 0.5055$). The mark rate data from the four upriver locations were therefore pooled (Table 9) and compared with those from Rampart; these rates were found to be significantly different ($P < 0.0001$).

Discussion

Our study provides convincing evidence that holding fall chum salmon in a live-box at the marking site negatively impacts their subsequent upriver migration. Fish holding time was positively related to the probability of recapture at Rampart in both 2001 and 2002. Similarly, travel time between the marking site and the Rampart site was lengthened by holding fish in 2001 and by crowding in 2002. We conjecture that the holding of fish elicits a stress response (e.g., Clements et al. 2002), causing fish to travel more slowly and closer to the bank, which thereby increases their probability of recapture in the Rampart fish wheel.

Although the increases in travel time and recapture probability at Rampart were statistically significant in both years, the magnitude of the increases was less in 2002 than in 2001. We suspect that the reduced sample size and changes made to operating protocols in 2002 (namely, holding fewer fish but substantially increasing the average holding time) caused the mean response to be less distinct. Fish response to holding may also depend on factors that we did not measure, such as water temperature or velocity, which differed between the 2 years. In any case, the effect was biologically meaningful in both years, and the conclusion that holding fall chum salmon in a live-box impairs their ability to migrate for at least some portion of time seems to be well founded.

Holding reduced the probability of fish recapture in the upriver sites (Beaver, Circle, and Canada DFO fish wheels) in 2001. One potential cause for that observation is an elevated mortality rate between the Rampart and upriver recapture sites, as Underwood et al. (2004) speculated. However, that finding was not repeated in 2002. Although we cannot explain the

TABLE 8.—Number (*N*) of adult Yukon River adult fall chum salmon captured by fish wheel and gill net at the recapture site near Rampart, Alaska, during corresponding periods of time within each of three temporal strata in 2003, and the number and proportion of those fish that had been marked at the two fish wheels near Tanana, Alaska.

	Gill net				Fish wheel		
Sampling period	Number of drifts	*N*	Number recovered	Mark rate	*N*	Number recovered	Mark rate
7–11 Aug	83	105	1	0.0095	122	1	0.0082
25–29 Aug	90	366	0	0.0000	319	0	0.0000
9–13 Sep	76	402	4	0.0100	900	9	0.0100

cause of this difference between years, we again suspect that holding fewer fish for longer periods in 2002 is partially responsible.

Substantial differences in the mark rates observed at the upriver recapture locations existed in both 2001 and 2002, and the rate at Rampart tended to exceed the rates observed upriver. The mark rates from Stevens Village and Beaver in 2002 represent the first estimates (based on adequate sample sizes) that were not substantially less than the rate observed at Rampart (Underwood et al. 2004), and they are intriguing for that reason. If capture and handling increase capture probabilities—as these results suggest—and subsequently increase the natural mortality rate, one would expect mark rates to reach a maximum at some location upriver from the marking site. That unknown location could be near one of the recapture sites but is arguably more likely to occur between sites and probably varies among years. In other words, elevated mark rates at Stevens Village and Beaver in 2002 could be caused by a continuation and magnification of the elevated capture probability observed at the Rampart site. However, several other plausible explanations can be constructed. Unfortunately, the interpretation of these two estimates is confounded by anomalies in the acquisition of these data. The estimated mark rate at Beaver in 2002 must be interpreted cautiously because the fish wheel was only effective in catching fish after being relocated during the later portion of the season. The 2002 Stevens Village mark rate estimate is suspect because approximately half of the recaptures at that site occurred over a short 4-d period. The resultant high mark rates observed at these locations seem unlikely to be representative of the entire migration at those points in the river. The degree of possible bias in these estimates and the significance of the lower mark rate observed at Rampart in 2002 relative to these sites cannot be assessed with confidence.

The results of this study are largely consistent with the findings of Underwood et al. (2004) and provide some additional support for their conclusions. Holding of fish, rather than the number of times a fish was captured, was associated with a reduced migration rate and increased capture probability at Rampart and with a reduced capture probability at upriver locations in 2001. The similarity of mark rates in the Rampart fish wheel and offshore gill-net catches in 2003 provides additional assurance that (1) the mark–recapture mixing assumption is not substantially violated and (2) the offshore-migrating subset of the population is susceptible to capture within the study area. The proportions of recaptured fish that were initially captured in the right-bank fish wheel tend to be similar to the proportion of all captures on the right bank, further suggesting that populations are mixed in the study area and that there is no bank orientation. The low mark rates observed in the Chandalar and Sheenjek rivers in 2003 are consistent with the findings of Underwood et al. (2004) and provide additional support for the hypothesis that mark rates are low in

TABLE 9.—Number (*N*) of adult Yukon River fall chum salmon captured at fish wheels near Rampart, Alaska, and Canada and sampled within three tributaries in 2003, and the number and proportion of those fish that had been marked at the two fish wheels near Tanana, Alaska.

Recapture location	Sampling period	*N*	Number recovered	Mark rate
Rampart	30 Jul–21 Sep	34,769	422	0.0121
Chandalar River	26 Aug–2 Oct	486	1	0.0021
	10 Oct	3,195	15	0.0047
Total	26 Aug–10 Oct	3,681	16	0.0042
Sheenjek River	11 Oct	190	1	0.0053
Fishing Branch River	30 Aug–19 Oct	924	6	0.0065
Canada	22 Aug–10 Oct	5,582	39	0.0070
All sites (excluding Rampart)		10,377	62	0.0060

all distant upriver locations. The similarity of mark rates observed within upper reaches of the drainage suggests that individual populations are not being tagged at substantially different rates. Finally, the digital photographs collected in 2002 provide physical evidence that tag loss within the main-stem Yukon River is very low or absent.

Although the results suggest that holding fall chum salmon in a live-box should be avoided, fish holding is clearly not solely responsible for the reduced mark rates observed at upriver locations. If holding was the sole factor, one would expect the proportion of catch consisting of immediately released (non-held) fish to be constant rather than to decline with distance from the marking site (Figure 3). In addition, although no fish were held at the marking site in 2003, mark rates at upriver locations were again found to be significantly lower than those at Rampart (Table 9). The cause of this difference has not been fully identified.

Two general explanations of the reduced mark rates are plausible: (1) undetected violations of the mark–recapture assumptions and (2) fish capture effects. There is little evidence to support the hypothesis that the effects are caused by violations of mark–recapture model assumptions. Tag loss within the Yukon River main stem or in tributaries below the spawning grounds appears to be essentially absent. In our study and other studies, tests of the assumption of mixing have failed to detect meaningful violations. All large fall chum salmon populations known to biologists have been monitored during the course of these studies, and mark rates from all populations have been similar and substantially less than those observed at Rampart. The study period of the mark–recapture investigation encompasses virtually the entire fall chum salmon migration, so an influx of a sufficiently large number of unmarked fish either before or after the study period is extremely unlikely. In addition, run reconstructions using independent data sources are similar to mark–recapture abundance estimates (Underwood et al. 2007); this implies that mark–recapture estimates are not substantially biased by assumption violations and that no large, unmonitored populations exist.

The second potential explanation is that one or more aspects (some yet unmeasured) of capturing, handling, and tagging fall chum salmon at the marking site elevate their mortality rate or substantially alter normal migratory behavior upriver of the mark–recapture study area. This explanation is supported by the findings that (1) mark rates at upriver locations tend to be substantially lower than those at Rampart, (2) mark rates tend to decline with distance from the marking site (Underwood et al. 2004), (3) holding time and fish crowding appear to negatively affect fish, and (4) fish caught in fish wheels more than once have reduced probabilities of recapture upriver of the mark–recapture study area (Underwood et al. 2004). The results of Underwood et al. (2004) indicate that capture itself may have an effect on the fish.

Some level of natural mortality certainly occurs during salmon migrations (Quinn 2005). Although mortality stemming from capture and handling is often assumed to occur for only a short time after release (e.g., Arnason and Mills 1987), a temporally persistent increased mortality rate is plausible. Such an increased mortality rate would cause mark rates to decline with distance from the marking site, as we observed and as was reported by Underwood et al. (2004). To our knowledge, other researchers have not documented such an effect (e.g., Cooke et al. 2006), although few investigators have sampled in numerous upriver locations. Yukon River fall chum salmon have one of the longest migrations of any chum salmon population in the world; some Yukon River populations migrate 3,200 km (Morrow 1980). An elevated mortality rate would be more detectable during a long migration. Although mortality has not been documented, available information implicates mortality as the most credible cause of the reduced recovery rates observed at upriver locations.

Additional investigations of the sort conducted to date are unlikely to provide additional insights into the cause of these phenomena. We have documented that holding fall chum salmon in live-boxes at the marking site should be avoided. Although holding fish was discontinued in 2003, other causative factors are clearly operating. Use of radiotelemetry could be successful in documenting mortality, but conducting a definitive telemetry study in a region of this size is a daunting challenge. One difficulty in conducting research of this type is obtaining a true control; fish that are studied must first be captured. If the capture event itself has an effect, then no true control can be obtained. Passive integrated transponder tagging of emigrating juveniles and use of a tag reader on both marking and recapture fish wheels during the return years would reduce the handling effect to that caused by fish wheel capture alone, but this would require a large number of juveniles to be tagged and would still not provide an uncontaminated control.

If fish wheel capture and tagging increase the mortality rate of fall chum salmon, one might hypothesize that the energy content of tagged fish at upriver locations would be less than that of untagged fish of a similar size and gender (Cleary 2003). Recently developed nonlethal methods of indexing the energy content of fishes have potential to advance our capabilities in this regard (Cox and Hartman 2005;

Crossin and Hinch 2005). A valid comparison between fish that have been captured and tagged and fish that have not been previously captured could be obtained by sampling tagged and untagged fish at an upriver location and comparing their energy reserves.

Acknowledgments

We would like to thank Stan Zuray, Paul Evans, Horace Smoke, the Stevens Village Natural Resources Department, Paul Williams, and Brian Asplund for operating the fish wheels used in this study. We would also like to thank Christine Apodaca (USFWS Fairbanks Fish and Wildlife Field Office) and the many members of the fish wheel, gill-net, and carcass sampling crews for their hard work and dedication to following operation protocols. Pat Milligan and Sandy Johnston (Canada DFO, Whitehorse, Yukon) have our sincere appreciation for sharing data collected during the course of their research. We also appreciate suggestions made by the anonymous reviewers, which greatly improved the clarity of the presentation.

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