Evidence of Residual Effects From the Capture and Handling of Yukon River Fall Chum Salmon in 2002

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by

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Abstract

In 2002, the U. S. Fish and Wildlife Service continued a study, initiated in 2001, of the effects of capturing Yukon River fall chum salmon (*Oncorhynchus keta*) in fish wheels, marking them with spaghetti tags, and releasing them to continue their migration. Two fish wheels were used to capture 5,518 fall chum salmon in the Yukon River mainstem approximately 50 km upriver of the Tanana River confluence. Fish were captured, tagged, and either released immediately (47.3%) or held in a live-box for as long as 9.6 h before being released. Fish were recaptured in fish wheels at five upriver sites near Rampart, Stevens Village, Beaver, and Circle, Alaska and in the mainstem near the international border in Canada. Mark rates of 3.0%, 4.6%, 3.0%, 1.6%, and 1.4% were observed at the five upriver locations, respectively. The mark rates observed at Stevens Village and Beaver are the first, from adequately sized samples, to be greater than or equal to that observed at the Rampart recapture site. However, the Beaver fish wheel caught few fish until it was moved late in the season, so the data may not be descriptive of the entire migration. Mark rates at the Circle and Canadian sites were substantially less than at the Rampart site, with the relative magnitude of the reduction similar to that observed in prior years. The reduced mark rates at upriver locations are a concern because they may reflect a violation of mark-recapture model assumptions or the impaired ability of captured fish to complete their migration. Possible causes of the differences in mark rates were investigated by modeling travel time and the probability of recapture as a function of measures of the conditions under which fish were captured and held. The length of time that fish were held in a live-box was positively associated with an increased probability of recapture at both the marking and Rampart recapture sites. In addition, a measure of crowding in a live-box was inversely related to the migration rate between the marking and Rampart recapture sites. These results are similar to those obtained in 2001. However, contrary to findings in 2001, the probability of recapture at the recapture sites upriver from Rampart was not significantly related to the conditions under which fish were held. Although holding fall chum salmon in a live-box appears to negatively affect their ability to migrate for at least some portion of time, measures of the conditions under which fish are held do not fully explain the reduced mark rates observed at the more distant upriver locations, and we recommend continued efforts to investigate potential causes.

Introduction

The Yukon River originates in the coastal mountains of northern British Columbia and flows over 3,200 km through British Columbia, Yukon Territory, and Alaska to empty into the eastern Bering Sea, draining an area of over 850,000 km^2 (Figure 1; Brabets et al. 2000). The Yukon River drains portions of the Brooks Range, the Alaska Range, the Wrangell-St. Elias Range, and numerous smaller mountain ranges. Five species of Pacific salmon (*Oncorhynchus* spp) spawn within the Yukon River drainage, although chinook (*O. tshawytscha*) and chum (*O. keta*) salmon are most abundant.

Two genetically distinct races of chum salmon occur within the Yukon River (Seeb and Crane 1999). Summer chum salmon tend to enter the river in June and July and spawn in tributaries of the lower and middle portion of the main-stem. Fall chum salmon tend to enter the Yukon River from July through mid-September and spawn in areas of upwelling ground water in the middle and upper portions of the drainage. Important fall chum salmon spawning areas include portions of the Tanana, Chandalar, Porcupine, and Kluane rivers, and the Canadian Yukon River main-stem (Barton 1992).

Fall chum salmon support important commercial and subsistence fisheries in the U. S. and commercial and First Nation fisheries in Canada. Buklis (1999) describes the recent history of U. S. commercial fisheries in northern and western Alaska, including the Yukon River. The 1996-2000 average harvests in the U. S. and Canada are 116,953 and 15,316, respectively (Vania et al. 2002), although this time period includes years of reduced returns and fishery restrictions. The primary goal of Yukon River salmon management is to maintain the abundance of spawning populations in selected spawning locations throughout the drainage (Vania et al. 2002). However, most fisheries occur large distances from the spawning grounds and there can be a substantial delay before the consequences of management decisions are observed on the spawning grounds. The ability of management to achieve the spawning goals is greatly increased by the availability of in-season estimates of abundance downstream of or near the areas where fisheries occur.

Several important fall chum salmon spawning populations have been monitored near their spawning grounds for many years, but in-season estimation of abundance in the mainstem Yukon River has only been achieved recently. Prior to 1995, the abundance of migrating fall chum salmon was estimated using sonar near Pilot Station, Alaska, a village in the lower Yukon River, by the Alaska Department of Fish and Game (ADFG; Pfisterer 2002) and with mark-recapture methods near the U. S.-Canada border by the Department of Fisheries and Oceans Canada (DFO; Johnson et al. 2002). The ADFG initiated a mark-recapture project to estimate the abundance of fall chum salmon in the upper Tanana River in 1995 (Cappiello and Bromaghin 1997). That project was expanded to include the Kantishna River drainage, a tributary of the Tanana River, in 1999 (Cleary and Bromaghin 2001). In 1996, the U. S. Fish and Wildlife Service (USFWS) initiated a mark-recapture project to estimate fall chum salmon abundance on the Yukon River mainstem above the Tanana River confluence near Rampart, Alaska (Gordon et al. 1998). The Tanana and Rampart projects provide important information from the middle portion of the Yukon River drainage, and have greatly improved the ability of managers to assess fall chum salmon abundance in-season and adjust harvest rates accordingly. The abundance estimates have become valuable for managing fall chum salmon, particularly in the middle and upper portions of the drainage where large subsistence fisheries occur, and have contributed to a better understanding of the relative magnitude of the upper Yukon River and Tanana River fall chum salmon populations.

In 1996, USFWS biologists associated with the Rampart mark-recapture project became aware that mark rates, i.e., the proportion of captured fish that have been marked, at Canadian research sites were substantially lower than mark rates observed at the project's recapture site near Rampart, Alaska. Subsequent investigations indicated a progressive reduction in mark rates as distance from the tagging site increased. Nine hypotheses regarding phenomena that could contribute to a reduction in mark rates were developed and the plausibility of each hypothesis was evaluated using available data (Underwood et al. 2000a, 2000b). Although the data were not conclusive, the potential cause judged to be most consistent with all available information was that the capture or tagging process increased the mortality rate between the recapture site near Rampart, Alaska and upriver locations. A similar effect would be produced by fish progressively exiting the migrating population and moving to, and perhaps even attempting to spawn in, unmonitored areas other than their original destination. Such a behavioral response and actual mortality will be referred to collectively as a prematurely-terminated migration (PTM).

The results of subsequent analyses of data collected in conjunction with the Rampart mark-recapture study continue to be inconclusive, but primarily consistent with a PTM hypothesis. Underwood et al. (2004b) documented a progressive reduction in mark rates with distance from the marking site, with samples being obtained from multiple locations and with several types of gear. 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 upriver locations, suggesting that simply being captured may be a causative factor and that the effects may be cumulative. Underwood et al. (2004b) concluded that the most plausible explanation of the observations was delayed mortality, i.e., the hypothesis of PTM.

The National Marine Fisheries Service (NMFS), in cooperation with the USFWS, conducted a radio telemetry study of Yukon River fall chum salmon in 1998 and 1999. Because a report detailing study results is not yet available, a summary of pertinent results follows (J. Eiler, National Marine Fisheries Service, personal communication). Fall chum salmon were tagged with transmitters at the marking site. The upriver migration of tagged fish was primarily monitored with fixed receiver stations (Eiler 1995), though a small number of aerial surveys were also flown. The results of this study provide mixed support to the PTM hypothesis. Although a small-scale experiment documented negative effects from holding fish prior to release, which is consistent with the PTM hypothesis, data on the final fate of radio-tagged fish were inconsistent between years. In 1998, most tagged fish were tracked to the upper mainstem Yukon River or tributaries known to contain fall chum salmon populations. However, in 1999, a relatively large proportion of radio-tagged fish appeared to remain in the Yukon River mainstem or small tributaries not thought to support populations of fall chum salmon. While this result is consistent with the PTM hypothesis, the magnitude of the effect is somewhat less than would be expected based on the mark-recapture data (Underwood et al. 2000a). The mark-recapture project documented substantial declines in mark rates in both 1998 (Underwood et al. 2004b) and 1999 (Tevis Underwood, USFWS, unpublished data). The cause of the difference in the telemetry results in 1998 and 1999, and the apparent discrepancies between the telemetry and mark-recapture projects, is unknown.

The potential for the Rampart mark-recapture project to increase fall chum salmon mortality is cause for concern. The fish wheel sites used in the project are locally known as productive sites. Annual catches at the marking and recapture sites have exceeded 18,000 and 40,000 chum salmon, respectively, and weekly estimates of capture probabilities have exceeded 0.10 and 0.15 at the two sites, respectively (Underwood et al. 2000a). An increase in mortality due to project operations therefore has the potential to affect a substantial number of fish and a substantial proportion of the population. Important fisheries, particularly subsistence and First Nation fisheries, occur in upper portions of the drainage, and it could be difficult to justify operation of an assessment project that may substantially elevate 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 project operations in 2000 (Underwood and Bromaghin 2003).

In 2001, the USFWS initiated a study to further investigate the declining mark rates of fall chum salmon upriver from the mark-recapture study area (Bromaghin and Underwood 2003). One objective of the study was to more rigorously document the reduced mark rates previously observed upriver from the Rampart recapture site. With the exception of data collected at Canadian research sites, upriver samples for mark rates had not been collected throughout the fall chum salmon migration (e.g., Underwood et al. 2004b). Because the mark-recapture study design called for a constant number of tagged fish to be released each day (e.g., Underwood et al. 2000a), one would expect mark rates to vary with abundance through time. In 2001, fish wheels were operated systematically throughout the duration of the run at two upriver locations, near Beaver and Circle, Alaska. The consistent collection of mark-rate data through the duration of the migration was expected to more conclusively document mark rates at these locations.

A second study objective of the study initiated in 2001 was to investigate the relationship between characteristics of the capture and handling of individual fish at the marking site and the probability of recapture in upriver locations (Bromaghin and Underwood 2003). Prior to 2001, sampling protocols of the mark-recapture study were designed only for purposes of abundance estimation (e.g., Underwood et al. 2004a). Once fish were captured by the fish wheel, most slid down a chute into a live-box, from which they were later removed, tagged, and released. The time tagged fish were released was recorded, but the time of capture could only be coarsely approximated. A relatively small number of fish were taken directly from the chute and processed without entering the live-box. In 2001, operations at the marking site were modified so that holding times were recorded with more precision. In addition, fish were intentionally held under a continuum of conditions, from being tagged and immediately released to being tagged and held for several hours, potentially under crowded conditions. The increased precision with which holding times were recorded allowed the probability of recapture in upriver locations to be modeled as a function of holding time. The objective of this component of the study was to identify handling practices associated with decreased recapture rates so that such practices might be avoided in future studies.

In 2001, Bromaghin and Underwood (2003) found that mark rates observed at upriver recapture sites were significantly less than at the Rampart recapture site, as had been previously observed (Underwood et al. 2004a). The length of time fall chum salmon were held in a live-box was associated with an increased probability of recapture at both the marking site and the Rampart recapture site, as well as with a reduced migration rate between those two sites. Conversely, the length of time fish were held was associated with a decreased probability of recapture at locations upriver from the Rampart recapture site. Bromaghin and Underwood (2003) speculated that one possible explanation of the results is that holding fish impairs their ability to migrate, leading to slower swimming speed and elevated recapture rates within the traditional mark-recapture study area, and that marked fish progressively exit the migrating population upriver of the Rampart recapture site, i.e., the PTM hypothesis. However, Bromaghin and Underwood (2003) noted that the magnitude of the effect of holding fish in a live-box was inadequate to fully explain the observed decline in mark rates.

The study initiated in 2001 was continued in 2002. The objectives of the study were largely unchanged, to more fully document mark rates upriver from the mark-recapture study area and investigate potential causes of the reduced mark rates. Whether or not the 2001 results would be replicated was, of course, also of interest. Because of the reduction in mark rates between the Rampart and Beaver recapture sites noted in 2001 (Bromaghin and Underwood 2003), an additional fish wheel was added near Stevens Village, roughly midway between Rampart and Beaver, in 2002. Digital photographs were taken from a subsample of fish captured in each location to enhance documentation of the lack of tag loss previously reported (Underwood et al. 2004b), as well as to generally document the condition of the primary and secondary mark locations. Finally, methods were modified slightly to increase the holding time for some fish with the intent to magnify the effect observed in 2001.

Study Area

The Rampart mark-recapture experiment was conducted on the Yukon River mainstem between its confluence with the Tanana River and the village of Rampart, Alaska (Figure 2; Underwood et al. 2004a). The marking site was located approximately 50 km above the Tanana River confluence, in an area known locally as 'The Rapids'. The river in this area exhibits a single deep channel and swift current. The recapture site was 52 km upriver near Rampart, Alaska.

Three additional recapture fish wheels were operated on the Yukon River mainstem upriver of the Rampart recapture site, approximately 211 km, 323 km and 531 km from the marking site near Stevens Village, Beaver and Circle, Alaska, respectively. Two fish wheels used by DFO in an independent mark-recapture study (e.g., Johnson et al. 2002), located approximately 793 km above the marking site near the international border in Canada, served as an additional recapture site.

Methods

Rampart Mark-Recapture Study

The core component of this investigation is the Rampart mark-recapture study that has been conducted annually since 1996 (Underwood et al. 2004a). The study is 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. A summary of operational methods is provided below; more detail is provided by Underwood et al. (2004a).

At the marking site, two fish wheels located on opposite banks of the river (Figure 2) were used to capture fish to be marked with individually numbered spaghetti tags. Operational plans called for up to 400 fish to be tagged daily, except Sundays when no fish were tagged. Fish processing consisted of determining sex from an examination of external morphology, measuring length from mid-eye to fork of tail to the nearest 1 cm, applying an individually numbered spaghetti tag, and removing the adipose fin as a secondary mark. All data were entered into a handheld data recorder. The times fish wheels were started and stopped and the times fish were captured and released were recorded to the nearest minute.

Fish were captured and processed during four daily tagging sessions, beginning at approximately 0800, 1200, 1600, and 1900 hours, 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 captured from the chute, processed, and placed into the live-box. Unmarked fish that fell into the live-box during a session were enumerated and their capture time was 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.

Fish held in a live-box during the first tagging session each day were released at the beginning of the second session; this procedure was implemented to increase the holding times for some fish each day. At the end of all other tagging sessions, the crew would revisit the first fish wheel and release the fish being held. All fish were released simultaneously by opening an underwater door in the live-box, allowing them to swim out of the live-box. The first wheel to be visited during a tagging session was alternated between sessions within a day and between the first session of consecutive days in an attempt to avoid potential bias caused by any differences between banks of the river or fish wheels.

A single fish wheel was used at the recapture site near Rampart, Alaska (Figure 2). The fish wheel was operated 24 hours a day, seven days a week. Crews tended the fish wheel from approximately 0500 hours to 2300 hours daily, with the exception of three one hour periods beginning at approximately 0900, 1300, and 1800 hours. 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 through the chute into the live-box and were subsequently removed by dip net. Fish accumulated in the live-box during times when the crew was not tending the fish wheel. Capture times for fish captured from the chute were recorded to the nearest minute. The time of capture for fish removed from the live-box was approximated as the midpoint between the earliest time the fish could have been caught and either the time the fish wheel was stopped or the time of release, whichever occurred first. Fish wheel start and stop times were usually reset every 1 h when the crew was present at the fish wheel, so capture times for most fish were recorded with variable precision that could range from near exact to within 0.5 h. The numbers of tagged and untagged fish caught, the tag number of tagged fish, and any incidence of tag loss were recorded.

Approximately 150 fish per week were sub-sampled for sex and length data at the recapture site. To reach this goal, fifty fish were measured during three days of the week (Monday, Wednesday, and Friday or Saturday). Digital photographs were taken of the first 15 fish captured each day to document the physical condition of the marks and any occurrence of tag loss.

Upriver Fish Wheel Operations

The effort with which the recapture fish wheels near Stevens Village, Beaver, and Circle, Alaska (Figure 2) were fished varied. Operational plans called for the Stevens Village fish wheel to operate 6 h per day, 7 days per week; the Beaver fish wheel to fish 10 h per day, 5 days per week; and the Circle fish wheel to operate 6 h per day, 5 days per week. The fish wheel contractors were to keep the wheels operating efficiently and monitor them while they were fishing. The date and time of fish wheel operations, the number of fish captured, the number of tagged fish recaptured, and any incidence of tag loss were recorded. Digital photographs were taken of the first 15 fish captured each day to document the physical condition of the marks and any occurrence of tag loss. Operators were allowed to harvest fish during legal fishery openings, though tagged and untagged fish were to be treated similarly to avoid changing the mark rate at upriver locations.

Two fish wheels used to mark fish in an independent mark-recapture experiment conducted by the DFO (Johnson et al. 2002) served as additional recapture fish wheels for this study. The fish wheels were located approximately 8 km apart on the right bank of the Yukon River mainstem near the international border in Canada (Figure 2). The fish wheels operated 24 hours each day, seven days per week, other than for brief periods during which the fish wheels required maintenance. Fish were captured and held in live-boxes, from which they were removed, tagged, and released during three daily tagging sessions. Canadian biologists examined each fish for the presence of primary and secondary marks (Pat Milligan, Fisheries and Oceans Canada, personal communication).

Data Analysis

Holding time at the marking site was computed as the time between capture and release. A measure of crowding for each fish was computed as the summed overlap in holding time with all other fish present in the live-box. Travel time between sites was computed as the time between the last release at a downriver site and the first capture at an upriver site. Travel time between the Rapids marking and Rampart recapture sites 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.

The probability of recapture and travel time were modeled using generalized linear models (Agresti 2002; McCulloch and Searle 2001). The probability of recapture was modeled as a binomial random variable with a logit link, while travel time was modeled as an inverse Gaussian random variable with an identity link (Zabel 1994). Explanatory variables considered for inclusion in the models included fish sex 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. The weekly strata defined at the marking site were utilized as categorical nuisance parameters to coarsely adjust for possible temporal changes in factors such 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 of version 8.02 of SAS STAT (SAS Institute Inc. 1999).

For each response variable, the analysis began by fitting a model including the 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 eliminated from the model until the remaining parameters were estimable. Likelihood ratio tests (Stuart et al. 1999) were then 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 were 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 to define statistical significance during model development.

Evaluating the fit of any model to data is an important phase of model development, particularly when a relatively large number of explanatory variables are being considered or models are otherwise complex. Statistical significance is not equivalent to a biological importance, e.g., Burnham and Anderson (2002), and failure to evaluate model fit can lead to unnecessarily complicated models or poorly-founded conclusions. A variety of methods were used to evaluate model fit. Whenever possible, models were graphically compared to data, or data summaries, to ensure that models were detecting observable features of the data.

A test that marked fish mix from bank to bank between the marking site and the Rampart recapture site is conducted annually as a routine component of the mark-recapture data analysis (Underwood and Bromaghin 2003). Additional insight into mixing or a bank effect can be obtained by comparing the proportions of fish tagged at a particular bank for fish recaptured at particular locations (Bromaghin and Underwood 2003). Such an analysis, for example, could reveal that certain populations prefer one bank to the other at the marking site. The bank at which a fish was first tagged was identified for each fish recaptured at each recapture site. For fish recaptured at a particular location, the hypothesis that the proportion that were tagged at the right bank fish wheel was equal to the overall proportion of all fish tagged at the right bank fish wheel was tested using an exact binomial test (Agresti 2002; Hollander and Wolfe 1999). A separate, identical, hypothesis was tested for each recapture location. Fish that escaped before their tag number, and therefore bank of tagging, could be determined were excluded from the analysis.

Mark rates observed in prior years (e.g., Underwood et al. 2004b) have consistently decreased as the distance from the marking site increased. If the decline was solely attributable to the effects of holding chum salmon in a live-box, the proportion of a catch comprised of marked fish that were not held should be equal at all recapture sites. To investigate this possibility, marked fish that were recaptured at each recapture site were classified according to whether or not they had been held. The proportions of each catch consisting of any marked fish, marked fish that had been held, and marked fish that had not been held were computed. A generalized linear model (Agresti 2002; McCulloch and

Searle 2001), with distance from the marking site as an explanatory variable, was fit to each of these three sets of proportions using a logit link and a binomial error distribution in order to compare the estimated coefficients of distance.

Results

Catch Statistics

Fish wheels at the marking site operated from 29 July to 14 September, releasing 5,518 tagged chum salmon (Table 1). Of these 5,518 fish, 42.7% were released from the fish wheel on the right (north) bank of the river and 47.7% percent were released without being held in a live-box. For the 2,888 fish that were held, holding times ranged from 0.5 to 9.6 h, with a mean of 2.7 h, and the measure of crowding ranged from 1.1 to 466.8 fish-h, with a mean of 87.6 fish-h. Females constituted 51.1% of the tagged fish. Female lengths ranged from 48 cm to 69 cm, while male lengths ranged from 48 cm to 72 cm Underwood et al. 2004a).

The recapture fish wheel at Rampart caught 14,478 chum salmon from 30 July to 18 September, 434 of which were recaptures. The Stevens Village recapture fish wheel captured 1,441 chum salmon, including 66 recaptures, from 22 August to 25 September. The Beaver recapture fish wheel operated from 8 August to 25 September, catching 559 chum salmon, 17 of which were tagged. The Beaver fish wheel caught very few fish prior to 5 September, when it was moved to a site that proved to be move productive. The Circle recapture fish wheel operated from 16 August through 1 October, catching 902 fish, 14 of which were tagged. The DFO fish wheels captured 5,578 chum salmon, 79 of which were tagged, from 26 July to 7 October (Pat Milligan, Fisheries and Oceans Canada, personal communication). Daily catches at all locations are presented in Table 1. For those fish caught more than once at a single location, only the last release at the marking site and the first occurrence at the recapture sites are included. Capture histories of 5,504 individual fish with complete data are summarized in Table 2; individuals were captured as many as three times. No tag loss was observed at any of the recapture sites. Travel time statistics for fish recaptured at each location are presented in Table 3; missing data prevented the travel time from being determined for all recaptured fish.

Mark rates observed at each recapture site are presented in Table 4 and plotted versus distance from the marking site in Figure 3. Mark rates were computed using only the first recapture of tagged fish caught more than once at a single location. Relative to the mark rate observed at the Rampart recapture site, the point estimate of the mark rate increased by 53% at Stevens Village, was essentially unchanged at the Beaver recapture site, and decreased approximately 50% at the Circle and Canadian Border recapture sites.

Digital photographs of 481, 401, 221, and 252 chum salmon were obtained from the

Rampart, Stevens Village, Beaver, and Circle recapture sites, respectively. No incidence of tag loss was documented and both primary and secondary marks were clearly distinguishable.

Modeling Data From the Marking Site

For the 270 marked fish caught more than once at the Rapids marking site, the first recapture of each fish was identified and the probability of recapture for the 5,505 fish with complete data was modeled using generalized linear models, as previously described. The initial model contained terms for the four-way interaction of sex, length, holding time, and the measure of crowding, all interactions of lower order, and all main effects. Because only the first time a fish was recaptured was of interest, the number of times fish were captured was not used in the model. The final model contained a common intercept for all marking strata and a term for holding time, i.e.,

$$E\left[\log\left(\frac{p_M}{1-p_M}\right)\right] = \beta_0 + \beta_1 H, \qquad (1)$$

where p_M = the probability of recapture at the marking site,
β_0 = intercept parameter,
β_1 = holding time parameter,
H = holding time, and

E[x] denotes the mathematical expectation of x (Hogg and Craig 1978). Estimation of the model parameters is summarized in Table 5. The estimated parameter for holding time is positive, indicating that holding time and probability of recapture are positively related. To evaluate model fit, nonzero holding times were placed into 1 h bins, with fish that were not held forming an additional classification (Table 6), and the proportion of fish in each bin that were recaptured was plotted with the estimated model in Figure 4. While the parameter for holding time is statistically significant (Table 5), the model does not fit the data very well (Figure 4) and the evidence that holding fish increases the probability of recapture at the marking site is not particularly strong.

All but the most simple generalized linear models of the time between the release of tagged fish and their first recapture at the marking site failed to converge. The most likely causes of convergence failure are high levels of variability or lack of structure in the data, or that the assumed inverse Gaussian distribution provided a poor model. Because holding time was positively associated with an elevated probability of recapture (Table 5), a generalized linear model containing a single intercept and a holding time parameter was fit to the data. The model provided a poor representation of the data (χ^2 =

0.2, df = 1, $P_\alpha = 0.6367$). No further analysis of these data was attempted.

Modeling Data From the Rampart Recapture Site

Data from 5,504 fish with complete records were used to model the probability that a tagged fish was recaptured at the Rampart recapture site. The analysis began with a model containing a five-way interaction of all the explanatory variables and all lower order terms. Eliminating insignificant terms led to a final model containing an intercept for each marking stratum and terms for sex and holding time, i.e.,

$$E\left[\left(\frac{p_{Ri}}{1-p_{Ri}}\right)\right] = \beta_{0i} + \beta_1 S + \beta_2 H, \qquad (2)$$

where p_{Ri} = the probability of recapture at Rampart for fish released in Marking Stratum i,
β_{0i} = intercept parameter for fish released in Marking Stratum i,
β_1 = sex parameter,
S = indicator of fish sex, female = 1 and male = 0,
β_2 = holding time parameter, and
H = holding time.

Estimation of the model parameters is summarized in Table 7. The estimated parameter for holding time is significantly greater than zero, indicating that increased holding time is associated with an increased probability of recapture.

To evaluate the fit of the model to the data, holding times greater than zero were binned into six, 1 h intervals. Those fish released without being held in the live-box, therefore with holding times of zero, formed an additional classification. The proportion of fish that were recaptured at Rampart was computed within each combination of a marking stratum and a holding-time category for each sex. Sample sizes, observed proportions, and binomial standard errors are presented in Table 8 for female chum salmon and in Table 9 for male chum salmon. Observed proportions and normal-approximation 95% confidence limits are compared to the final generalized linear model in Figure 5 through Figure 11. There is a general tendency for recapture rates to increase with holding time in both the observed data and the estimated model, though the effect is not ubiquitous or extremely strong.

The analysis of travel time data between the marking site and the Rampart recapture site also began with a model containing a five-way interaction of the explanatory variables and all lower order terms. Stepwise elimination of nonsignificant terms ended with a final model containing an intercept for each marking stratum and a term for the measure of crowding in a live-box, i.e.,

$$E\left[T_i\right] = \beta_{0i} + \beta_1 C , \qquad (3)$$

where T_i = the travel time to the Rampart recapture site for fish released in Marking Stratum i,

β_{0i} = intercept parameter for fish released in Marking Stratum i,

β_1 = crowding parameter, and

C = measure of crowding.

The parameter estimate for the measure of crowding was positive (Table 10), indicating that holding fish under crowded conditions was positively related to the mean travel time to the Rampart recapture site. The estimated model for the mean travel time is plotted with the observed data, by stratum, in Figure 12.

The apparent effect of holding fish on the probability of recapture at the Rampart recapture site has the potential to negatively bias the mark-recapture abundance estimate (Bromaghin and Underwood 2003). For that reason, we estimated abundance using the methods of Underwood et al. (2004a), but treating only those fish that were not held as marked fish. The resulting abundance estimate was 274,692 fish with a standard error of 43,210. Although the point estimate is approximately 40% greater than that reported by Underwood et al. (2004a), the reduced sample sizes led to greatly increased variance and the estimates are not statistically different.

Modeling Data From Upriver Recapture Sites

Because of the small number of fish recaptured at the Stevens Village, Beaver, Circle, and Canadian Border sites, no analysis of travel times was attempted. Generalized linear models of the probability of recapture were fit to the data from the Stevens Village recapture site, but none of the explanatory variables remained in the final model. No models were fit to the data from the Beaver recapture site because the fish wheel caught very few fish until it was moved midway through the season. Because no substantial fall chum salmon spawning tributaries are known to occur between the Circle and Canadian Border recaptures sites and no fish were captured in both locations (Table 2), these sites were pooled and treated as a single recapture location for modeling. However, as with the Stevens Village data, no measures of capture or handling at the marking site were significantly related to the probability of recapture at the combined locations.

Analysis of Bank of Initial Tagging

Of the 5,518 fall chum salmon tagged at the marking site, 42.7% were tagged at the right-bank fish wheel. For the tagged fish recaptured at each of the recapture sites, the hypothesis that 42.7% of them had been tagged at the right-bank fish wheel was tested using an exact binomial test, as previously described. Observed proportions, exact 95% confidence interval limits, and the p-values of the tests are presented in Table 11; the proportions and confidence intervals are plotted in Figure13. None of the tests were significant, implying that there is no evidence that a bank effect is responsible for the differences in mark rates at the recapture sites.

Analysis of Mark Rates

The results of fitting generalized linear models to the proportions of a catch consisting of any marked fish, marked fish that were held, and marked fish that were not held are presented in Table 12. Although the estimated coefficient of distance for fish that were not held is substantially greater than for fish that were held, which is consistent with the hypothesis that holding fish contributes to the decline in mark rates, the coefficients are not significantly different. The coefficient of distance for fish that were not held is also significantly less than zero, suggesting that the proportions of the catches consisting of such fish are not equal. The estimated models and the observed data are plotted in Figure 14. To aid comparison of the models, they were standardized to have a proportion of 1.0 at a distance of 0 and plotted in Figure 15.

Discussion

Recapture Probability and Travel Time

The results of this study provide additional documentation that holding fish in a live-box at the Rapids marking site negatively impacts their subsequent upriver migration. The length of time fish were held in a live-box was positively related to the probability of recapture at the marking site (Table 5, Figure 4) and at the Rampart recapture site (Table 7, Figures 5-11). Similarly, the measure of crowding in a live-box was positively related to the travel time between the marking site and the Rampart recapture site (Table 10, Figure 12). These results are similar to the results of the 2001 study (Bromaghin and Underwood 2003), although the magnitude of the effect seems somewhat reduced. Changes made to the 2002 study design to increase the range of holding times, in combination with the substantial reduction in the proportion of fish that were held, 71% in 2001 (Bromaghin and Underwood 2003) versus 52.3% in 2002, may have made the effect less distinct. It is also possible that the magnitude of the effect depends partially on factors that have not been measured. In any case, an effect is observable in both years and the conclusion that holding chum salmon in a live-box impairs their ability to migrate for at least some period of time seems well founded.

No statistically significant relationship between measures of holding chum salmon and the probability of recapture at sites upriver from the Rampart site were observed in 2002. This is in conflict with the 2001 results, which clearly indicated that the length of time fish were held was inversely related to the probability of recapture at the upriver sites (Bromaghin and Underwood 2003). The reasons underlying this difference between years are unknown. It is possible that the relationship simply did not exist in 2002. However, similar to the reduced magnitude of the effects observed at the Rampart recapture site in 2003, the reduced sample size and greater range of holding time in 2002 may have precluded identification of an effect within the rather variable data.

Differences Among Mark Rates

Substantial differences in mark rates were observed among the five recapture sites (Figure 3). As in past years, mark rates observed at the Circle and Canadian Border sites were substantially less than that observed at the Rampart site (Underwood et al. 2004b; Bromaghin and Underwood 2003). However, in 2003, the mark rate observed at the Stevens Village site was substantially greater than that at the Rampart site, and the mark rate at the Beaver site was approximately equivalent to that at the Rampart site. In 2001, the mark rate at the Beaver site was approximately 50% of that observed at the Rampart site, which motivated adding the Stevens Village fish wheel in 2002 (Bromaghin and Underwood 2003).

The estimated mark rates from the Stevens Village and Beaver recapture sites are the first two estimates from adequately-sized samples taken anywhere upriver of the Rampart recapture site that have been as great or greater than the mark rate observed at Rampart, and they are intriguing for that reason. Elevated recapture probabilities at these locations could be caused by a magnification of the effect observed at the Rampart site, or by heterogeneity in capture probabilities at the marking site. Unfortunately, the interpretation of the Stevens Village and Beaver mark rate data is complicated by operational details and certain characteristics of the data. As noted previously, the Beaver mark rate should be viewed with some skepticism because the wheel was not operating efficiently until it was moved to a new location midway through its operational period (Table 1). In effect, this fish wheel only sampled the second half of the migration. With respect to data from the Stevens Village recapture site, approximately 50% of the 66 recaptured fish were captured during a 4-day period in late August (Table 1), which alone casts some doubt on the reliability of the estimated mark rate. Coincidently, estimated capture probabilities at the marking site were relatively large during a two week period that would correspond with the late August period at the Stevens Village site and the very beginning of the period following the movement of the Beaver fish wheel (Underwood et al. 2004a). Given these qualifications, the mark rates from the Stevens

Village and Beaver recapture sites may have substantial bias and should be viewed with some skepticism. The degree to which the estimates are biased and the significance of the fact that they exceed the mark rate observed at the Rampart recapture site can not be assessed with confidence.

Setting aside the veracity of the mark rates observed at the Stevens Village and Beaver sites, the mark rates observed at the Circle and Canadian Border sites are significantly less than the mark rate observed at the Rampart site (Table 12, Figure 14). Although the decline is less severe than in 2001 (Bromaghin and Underwood 2003), the disparity between fish that were and were not held appears to be greater in 2002 (Figure 15). The observations of reduced mark rates at upriver locations are a concern because of the gravity of the most likely causes. Three factors have the greatest potential of producing a decline of the observed magnitude: tag loss, one or more violations of the related mark-recapture assumptions regarding heterogeneity in capture probabilities and the mixing of tagged and untagged fish, and tagged fish dropping out of the migrating population through delayed mortality or a non-fatal but progressive stress-induced response (the PTM hypothesis).

The decline in mark rates is unlikely to have been caused by tag loss. A secondary mark has been used in most prior years and both crews and fish wheel operators were made aware of the importance of examining fish for the presence of the secondary mark (Underwood et al. 2004b). Many thousands of fish have been examined for the presence of primary and secondary marks since the mark-recapture study was initiated in 1996. No incidence of tag loss has been conclusively documented from fall chum salmon captured in the main-stem Yukon River since the inception of the mark-recapture project, though one instance was reported during an interview of a fisher from Beaver, Alaska (Underwood et al. 2004b). In particular, fall chum salmon captured in the Canadian Border fish wheels are tagged in an independent mark-recapture study that also uses spaghetti tags, and large-scale tag loss would almost certainly have been noticed by the Canadian tagging crew. Tag loss was not observed among the 1,355 chum salmon that were digitally photographed from the four U. S. recapture sites. If tag loss was occurring at the magnitude necessary to explain the observed decline in mark rates, it is difficult to imagine that documentation of tag loss would be essentially absent.

One might hypothesize that differences in mark rates are attributable to a violation of the mark-recapture assumptions that all fall chum salmon have equal capture probabilities and that marked and unmarked fish mix completely prior to the recapture event (Seber 1982). It is possible that fish within the confines of the mark-recapture study area are segregated such that different components of the migrating population are tagged at different rates. Differences in mark rates would then be caused by either increased segregation or protracted mixing of the components upriver from the Rampart recapture site. Although this hypothesis is difficult to directly test, it is not supported by the available evidence. This hypothesis would imply that some components of the migration are tagged at a rate somewhat greater than the mark rate observed at the Rampart recapture site, and that other components are tagged at reduced rates. However, with the exception of few small samples and the Stevens Village and Beaver data from 2002, all mark rates observed at locations upriver from the Rampart recapture site have been less than that observed at the Rampart site (Underwood et al. 2004b). Furthermore, these samples have been obtained in several years using a variety of gear types and in numerous locations, including all the known primary spawning grounds upriver from the mark-recapture study area (Underwood et al. 2004b). Annual tests of between-bank mixing of tagged fish between the marking and Rampart recapture sites suggest that tagged fish mix between the two locations (e.g., Underwood and Bromaghin 2003). Collectively, this body of evidence provides reasonable assurance that model assumptions have not been violated in such a fashion.

Mark-recapture model assumptions could be violated if stocks of fall chum salmon are differentially segregated by bank, which has been observed in the Yukon River main-stem below the confluence of the Tanana River (Buklis 1981; Spearman and Miller 1997). However, the results of this study provide some assurance that this did not occur within the study area in 2002. If stocks were differentially segregated by bank, the proportion of fish tagged on a particular bank would differ between stocks. However, of the fish recaptured at upriver locations, the proportions that had been tagged on the right bank at the marking site were statistically indistinguishable from the proportion of all tagged fish tagged at the right bank (Figure 13), and similar results were obtained in 2001 (Bromaghin and Underwood 2003).

The third potential cause of the decline in the mark rates is the PTM hypothesis. Underwood et al. (2004b) suggested that mortality upriver of the Rampart recapture site is the most likely cause of the decline. They also found that recapture rates decreased as the number of times fish were captured in fish wheels increased, which suggests that the capture event itself may have negative effects on fish and that factors potentially causing PTM may be cumulative (Wedemeyer et al. 1990). We are not aware of any investigations that have conclusively documented a PTM effect from the capture of fall chum salmon in fish wheels. However, Cleary (2003) found there were metabolic costs associated with the fish wheel capture and tagging of migrating Tanana River fall chum. In addition, numerous studies have documented stress or mortality associated with the capture or handling of salmon or related species; recent examples include Buchanan et al. (2002), Budy et al. (2002), and Clements et al. (2002). While there is no conclusive evidence that capturing and handling migrating Yukon River fall chum salmon causes a PTM effect, that hypothesis seems more consistent with the body of available evidence than any other potential explanation.

Potential Implications to Management and Research

The results of this study raise questions regarding the use of fish wheels and live-boxes in fishery management. Use of fish wheels is common in some portions of the Yukon River drainage, and live-boxes have been viewed as a tool allowing the capture of target species and the live release of non-target species. In some years of low salmon abundance when subsistence fisheries were restricted, fish wheels could only be operated if a live-box was attached or if the fish wheel operator was present, so that non-target species could be released alive (e.g., Bergstrom et al. 1998). The release of fish from a live-box is certainly less harmful to the fish than the traditional 'dead-box', which is not submerged, but results from both years of study imply that live-boxes may not be as innocuous as was previously believed.

Fish wheels, many with live-boxes, have become a fairly common research platform within the Yukon River drainage, and elsewhere in Alaska (e.g., Kerkvliet and Hamazaki 2003; Savereide 2003; Underwood and Bromaghin 2003; Cleary and Hamazaki 2002; and Johnson et al. 2002). If the use of live-boxes was found to negatively affect salmon, the cost to research programs in terms of reduced sample sizes, increased personnel costs to actively monitor fish wheels, or the need to develop alternative capture techniques could be substantial. However, with the exception of Cleary (2003), other researchers that have investigated the effects of capturing and handling salmon using fish wheels have not obtained similar findings regarding recapture probability or travel time. Kerkvliet and Hamazaki (2003) did not observe differences among Kuskokwim River coho salmon held for different lengths of time. Cleary and Hamazaki (2002) found that Tanana River fall chum salmon with longer mean holding times sometimes had elevated migration rates, rather than reduced migration rates as observed in this study. The cause of the differences among these findings is unknown. The large sample sizes obtained in this study, or the increased precision with which holding time was measured, may have made the effect discernable. For example, the precision with which Kerkvliet and Hamazaki (2003) measured holding time is unclear, and they binned holding time into categories prior to analysis. However, other explanations are possible and the causes for the apparent differences between studies merits additional investigation.

The elevated capture probability of held fish at the Rampart recapture site has implications for the annual Rampart fall chum salmon mark-recapture study. Although protocols have been modified to reduce holding times in recent years, some fish have been held at the marking site in every year of the study (e.g., Underwood and Bromaghin 2003). An increased recapture probability for tagged fish is effectively a 'trap-happy' response, and it negatively biases abundance estimates (Seber 1982). Underwood et al. (2004a) reported that abundance estimates are less than run reconstructions based on all available upriver data sources in five of six years, though differences are relatively small and measures of precision of the data sources used in the run reconstruction are not generally available. Negative biases caused by holding fish might be responsible for the tendency of the estimates to be less than the run reconstructions. To avoid potential bias, abundance estimation should be based on data from fish that are not held. In 2002, the estimate of abundance increased by approximately 40% when data on held fish were excluded. However, the number of marked fish was reduced by approximately 50% and the standard error of the estimate increased by nearly 350%. For these reasons, although the point estimate was expected to increase, the magnitude of the increase must be viewed with caution.

Conclusions

The results from the two years of study conclusively document that holding Yukon River fall chum salmon in a live-box at the Rapids marking site increases their probability of recapture at that location, increases their travel time to the Rampart recapture site, and increases their probability of recapture at the Rampart site, all of which are consistent with the PTM hypothesis. These results also imply that historic estimates of fall chum salmon abundance obtained by the Rampart mark-recapture study are negatively biased, though the magnitude of the bias is difficult to determine with the available data.

Evidence that the effects of holding fall chum salmon in a live-box persist as they continue their migration above the Rampart recapture site were obtained in 2001 (Bromaghin and Underwood 2003), but that was not confirmed by findings in 2002. That negative effects persist through the migration in some years seems likely. However, in either case, holding fall chum salmon in a live-box clearly does not explain the reduction in mark rates observed at upriver locations. These results, in combination with the findings of Underwood et al. (2004b), suggest that negative and cumulative effects may be caused by the capture event itself, rather than holding conditions. The results of this study suggest that negative effects can be reduced, but not eliminated, by ceasing to hold fall chum salmon in a live-box.

The potential for use of fish wheels to impair the migratory fitness of Pacific salmon is a serious concern given their widespread use in fishery management and research. Work completed to date has provided valuable insights into the potential effects of fish wheels and has answered some questions, yet additional questions remain unanswered. Researchers using fish wheels to capture salmon are encouraged to continue investigations so that a full understanding of the effects of fish wheel capture on fish can be obtained as quickly as possible.

Recommendations

A continuation of this research is unlikely to provide new insights into the effects of fish wheels, so additional work of this type is not recommended. Results from 2001 and 2002 conclusively document that holding fall chum salmon in a live-box at the Rapids marking site increases the recapture probability of tagged fish at the Rampart recapture site, introducing a negative bias into abundance estimation. For that reason, use of live-boxes should be discontinued at the marking site.

As previously discussed, all the known spawning grounds upriver from the mark-recapture study area have been sampled, as have numerous mainstem locations, and nearly all mark rate estimates have been substantially less than estimates obtained at the Rampart recapture site. That fact adds some credence to the conclusion that spawning populations are not spatially segregated at the marking site. However, mark rate estimates from the Chandalar and Sheenjek rivers, two of the largest fall chum salmon populations, are only available from one year (Underwood et al. 2004b). While the mark rates observed in both tributaries in that year were quite low, it would be prudent to obtain additional data in at least one more year.

One possibility that has not yet been investigated is the potential segregation of fish on and off shore within the mark-recapture study area. Such a segregation could produce a progressive decrease in mark rate upriver from the mark-recapture study area if tagged and untagged fish gradually mix as they migrate upriver. One approach to investigating this possibility would be to compare the mark rates of fish captured in the Rampart recapture fish wheel and those captured in gill nets off shore at the same location. Given the relatively small mark rate observed in fish captured in the fish wheel, say 3% to 5%, it is likely that at least several hundred fish would need to be harvested in the gill nets. Given the reduced abundance of fall chum salmon in recent years and the importance of the fish to fishers, the implications to management and the disposition of the harvested fish need to be carefully evaluated prior to conducting such a study.

Further, consideration should be given to alternative methods of investigating causes for the differences in mark rates. Use of radio telemetry may be an option, but the high cost of tags and the immensity of the study area may reduce the attractiveness of this approach. Comparing genetic estimates of stock composition at the marking site with estimates of abundance from upriver data sources might provide useful insights into the potential for stock-based selectivity at the marking site, though available data is consistent with a lack of selectivity. In addition, the possibility of evaluating the effectiveness of alternative capture and marking methods at the marking site may have merit.

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Table 1. Number of tagged chum salmon released at the marking site and catches at the upriver recapture sites, by day (Page 1 of 3).

		Rampart		Stevens Village		Beaver		Circle		Canadian Border	
Date	Tags Released	Marked Catch	Total Catch	Marked Catch	Total Catch	Marked Catch	Total Catch	Marked Catch	Total Catch	Marked Catch	Total Catch
07/26										0	1
07/27										0	1
07/28										0	2
07/29	36									0	1
07/30	49	0	41							0	2
07/31	46	1	65							0	2
08/01	46	1	47								
08/02	28	0	40								
08/03	28	1	49							0	6
08/04		4	48							0	3
08/05	53	0	56							0	2
08/06	58	1	71							0	6
08/07	59	3	70							0	10
08/08	36	2	55			0	1			0	2
08/09	35	2	77			0	1			0	3
08/10	11	3	62							0	10
08/11		1	34							0	7
08/12	35	1	56			0	1			0	11
08/13	54	2	125			0	3			0	5
08/14	63	1	112			0	1			0	10
08/15	91	0	122			0	1			0	12
08/16	99	1	161			0	0	0	2	0	7
08/17	89	3	219							0	9
08/18		4	216							0	15
08/19	109	2	170			0	3	0	0	0	9

Table 1. Number of tagged chum salmon released at the marking site and catches at the upriver recapture sites, by day (Page 2 of 3).

		Rampart		Stevens Village		Beaver		Circle		Canadian Border	
Date	Tags Released	Marked Catch	Total Catch	Marked Catch	Total Catch	Marked Catch	Total Catch	Marked Catch	Total Catch	Marked Catch	Total Catch
08/20	110	3	177			0	1	0	0	0	11
08/21	133	1	180			0	2	0	2	0	9
08/22	159	6	147	0	20	0	0	0	3	0	14
08/23	202	4	194			0	1	0	2	0	20
08/24	218	6	170	0	18					0	22
08/25		12	140	1	27					0	26
08/26	153	14	167	1	28	0	0	0	1	0	27
08/27	142	13	225	0	30	0	2	0	11	0	9
08/28	193	24	324	9	61	0	0	0	31	0	19
08/29	254	17	369	10	61	0	1	0	47	0	22
08/30	267	12	418	7	98	0	1	0	32	0	26
08/31	276	21	459	9	69					0	39
09/01		23	517							0	70
09/02	232	19	593	3	56	0	0	0	52	0	84
09/03	255	13	602	7	77	0	1			0	77
09/04	261	19	664	1	68	0	0	0	44	0	46
09/05	268	18	862	2	61	1	14	2	31	0	178
09/06	238	33	974			2	25	1	35	0	134
09/07	273	25	779							2	136
09/08		24	849							1	187
09/09	165	11	833	4	95	4	72	1	38	2	195
09/10	204	12	548	2	89	2	54	1	43	3	226
09/11	168	13	666	0	55	3	57			3	185
09/12	139	21	603	1	106	2	71	3	57	2	225
09/13	100	14	325	2	108	0	56	2	53	1	221

Table 1. Number of tagged chum salmon released at the marking site and catches at the upriver recapture sites, by day (Page 3 of 3).

		Rampart		Stevens Village		Beaver		Circle		Canadian Border	
Date	Tags Released	Marked Catch	Total Catch	Marked Catch	Total Catch	Marked Catch	Total Catch	Marked Catch	Total Catch	Marked Catch	Total Catch
09/14	83	13	395	3	80			1	73	2	260
09/15		5	223	3	82					4	223
09/16		4	134	1	88	0	35	1	71	6	210
09/17		0	29	0	22	1	60	1	86	3	145
09/18		1	16	0	15	1	27	0	53	6	187
09/19				0	0	0	25	1	66	5	276
09/20				0	18	1	23	0	3	5	358
09/21				0	5					6	276
09/22				0	2					7	238
09/23				0	0	0	9	0	19	3	182
09/24				0	1	0	5	0	23	3	164
09/25				0	1	0	6	0	11	2	111
09/26								0	8	1	149
09/27										3	80
09/28										0	58
09/29								0	3	0	96
09/30								0	2	2	56
10/01								0	0	1	40
10/02										0	34
10/03										1	34
10/04										4	31
10/05										1	23
10/06										0	2
10/07										0	1
Total	5,518	434	14,478	66	1,441	17	559	14	902	79	5,578

Table 2. Number of chum salmon with complete capture records, by capture history.

Number Of Fish	Number of Times Fish Were Captured at Each Location: Marking Site	Rampart	Stevens Village	Beaver	Circle	Canadian Border	Total
4,679	1	0	0	0	0	0	1
65	1	0	0	0	0	1	2
1	1	0	0	0	0	2	3
12	1	0	0	0	1	0	2
14	1	0	0	1	0	0	2
53	1	0	1	0	0	0	2
1	1	0	1	0	0	1	3
389	1	1	0	0	0	0	2
3	1	1	0	0	0	1	3
1	1	1	0	0	0	2	4
1	1	1	0	0	1	0	3
1	1	1	0	1	0	0	3
6	1	1	1	0	0	0	3
8	1	2	0	0	0	0	3
1	1	3	0	0	0	0	4
231	2	0	0	0	0	0	2
1	2	0	0	0	0	1	3
4	2	0	1	0	0	0	3
17	2	1	0	0	0	0	3
1	2	1	0	0	0	1	4
12	3	0	0	0	0	0	3
3	3	1	0	0	0	0	4

Table 3. Summary travel time statistics, in days, between the Rapids marking site and upriver recapture sites.

Recapture Location	Distance (km)	Number Of Fish	Mean	Standard Deviation	Minimum	Maximum
Rampart	52	431	2.5	2.1	1	19
Stevens Village	211	64	5.2	2.1	3	12
Beaver	323	15	7.9	1.1	7	11
Circle	531	13	16.8	3.2	12	23
Canadian Border	793	73	22.7	4.2	16	34

Table 4. Sample sizes and inferential statistics for mark rates, by recapture location.

Recapture Location	Sample Size	Number Marked	Proportion Marked	Standard Error	95% C. I. Limits Lower	95% C. I. Limits Upper
Rampart	14,478	434	0.0300	0.0014	0.0272	0.0328
Stevens Village	1,441	66	0.0458	0.0055	0.0350	0.0566
Beaver	559	17	0.0304	0.0073	0.0162	0.0447
Circle	902	14	0.0155	0.0041	0.0074	0.0236
Canadian Border	5,578	79	0.0142	0.0016	0.0111	0.0173

Table 5. Parameters and inferential statistics of the generalized linear model of the probability a tagged chum salmon was recaptured at the Rapids marking site.

Parameter	Estimate	Standard Error	Chi-square Test Statistic	Degrees Of Freedom	Significance
Intercept	-3.0818	0.0832	1371.0	1	< 0.0001
Holding Time	0.0807	0.0353	5.2	1	0.0222

Table 6. Summary statistics of the proportion of tagged chum salmon that were recaptured at the Rapids marking site, classified by binned categories of holding time in a live-box.

Holding Time (h)	Sample Size	Proportion Recaptured	Standard Error
0	2,668	0.0476	0.0041
0 - 1	306	0.0229	0.0086
1 - 2	918	0.0316	0.0058
2 - 3	710	0.0718	0.0097
3 - 4	200	0.0700	0.0181
4 - 5	455	0.0681	0.0118
5 - 6	248	0.0444	0.0131

Table 7. Parameters and inferential statistics of the generalized linear model of the probability a tagged chum salmon was recaptured at the Rampart recapture site.

Parameter	Estimate	Standard Error	Chi-square Test Statistic	Degrees Of Freedom	Significance
Intercept - Stratum 1	-3.2858	0.3460	90.2	1	< 0.0001
Intercept - Stratum 2	-2.9709	0.2918	103.6	1	< 0.0001
Intercept - Stratum 3	-3.1181	0.2455	161.3	1	< 0.0001
Intercept - Stratum 4	-2.6004	0.1405	342.5	1	< 0.0001
Intercept - Stratum 5	-2.3495	0.1160	410.0	1	< 0.0001
Intercept - Stratum 6	-2.4448	0.1160	444.1	1	< 0.0001
Intercept - Stratum 7	-2.3177	0.1360	290.4	1	< 0.0001
Sex (Female)	-0.2281	0.1013	5.1	1	0.0243
Holding Time (h)	0.1031	0.0272	14.3	1	0.0002

Table 8. Summary statistics of the proportion of tagged female chum salmon that were recaptured at the Rampart recapture site, jointly classified by marking stratum and binned categories of holding time in a live-box (Page 1 of 2).

Holding Time (h)	Statistic	Stratum 1	Stratum 2	Stratum 3	Stratum 4	Stratum 5	Stratum 6	Stratum 7
	Sample Size	53	55	114	213	325	387	215
0	Sample Proportion	0.0000	0.0364	0.0351	0.0563	0.0738	0.0388	0.0651
	Standard Error	0.0000	0.0255	0.0173	0.0158	0.0145	0.0098	0.0169
	Sample Size	7	4	16	23	36	41	24
0 - 1	Sample Proportion	0.0000	0.0000	0.1250	0.0870	0.0833	0.1463	0.0417
	Standard Error	0.0000	0.0000	0.0854	0.0601	0.0467	0.0559	0.0417
	Sample Size	14	20	45	80	108	126	78
1 - 2	Sample Proportion	0.0714	0.0000	0.1111	0.0375	0.0741	0.0952	0.0897
	Standard Error	0.0714	0.0000	0.0474	0.0214	0.0253	0.0263	0.0326
	Sample Size	13	13	28	54	77	111	61
2 - 3	Sample Proportion	0.0769	0.0000	0.0714	0.0741	0.1039	0.1441	0.1148
	Standard Error	0.0769	0.0000	0.0496	0.0360	0.0350	0.0335	0.0411
	Sample Size	4	2	8	21	24	37	5
3 - 4	Sample Proportion	0.0000	0.0000	0.0000	0.0000	0.2083	0.0541	0.2000
	Standard Error	0.0000	0.0000	0.0000	0.0000	0.0847	0.0377	0.2000
	Sample Size	9	11	16	20	41	75	48
4 - 5	Sample Proportion	0.0000	0.0909	0.0625	0.1000	0.0976	0.0667	0.0208
	Standard Error	0.0000	0.0909	0.0625	0.0688	0.0469	0.0290	0.0208

Table 8. Summary statistics of the proportion of tagged female chum salmon that were recaptured at the Rampart recapture site, jointly classified by marking stratum and binned categories of holding time in a live-box (Page 2 of 2).

Holding Time (h)	Statistic	Stratum 1	Stratum 2	Stratum 3	Stratum 4	Stratum 5	Stratum 6	Stratum 7
	Sample Size	2	6	17	19	18	47	27
5 - 6	Sample Proportion	0.0000	0.0000	0.0000	0.2632	0.1667	0.0851	0.1481
	Standard Error	0.0000	0.0000	0.0000	0.1038	0.0904	0.0411	0.0697
	Sample Size	0	0	0	0	2	2	0
6 - 7	Sample Proportion					0.0000	0.0000	
	Standard Error					0.0000	0.0000	
	Sample Size	1	0	0	0	2	2	2
7 - 8	Sample Proportion	0.0000				0.0000	0.0000	0.5000
	Standard Error					0.0000	0.0000	0.5000
	Sample Size	0	0	0	0	0	0	0
8 - 9	Sample Proportion							
	Standard Error							
	Sample Size	0	1	0	0	1	0	0
9 - 10	Sample Proportion		0.0000			0.0000		
	Standard Error							

Table 9. Summary statistics of the proportion of tagged male chum salmon that were recaptured at the Rampart recapture site, jointly classified by marking stratum and binned categories of holding time in a live-box (Page 1 of 2).

Holding Time (h)	Statistic	Stratum 1	Stratum 2	Stratum 3	Stratum 4	Stratum 5	Stratum 6	Stratum 7
	Sample Size	57	65	83	233	298	324	194
0	Sample Proportion	0.0526	0.0769	0.0000	0.0858	0.0638	0.0741	0.1082
	Standard Error	0.0298	0.0333	0.0000	0.0184	0.0142	0.0146	0.0224
	Sample Size	7	6	3	26	46	47	24
0 - 1	Sample Proportion	0.0000	0.0000	0.0000	0.1154	0.1087	0.0426	0.0417
	Standard Error	0.0000	0.0000	0.0000	0.0639	0.0464	0.0298	0.0417
	Sample Size	18	26	40	92	93	120	66
1 - 2	Sample Proportion	0.0556	0.1154	0.1000	0.0543	0.1613	0.0917	0.1364
	Standard Error	0.0556	0.0639	0.0480	0.0238	0.0383	0.0265	0.0426
	Sample Size	17	20	19	69	83	78	48
2 - 3	Sample Proportion	0.0588	0.0500	0.0000	0.1014	0.0843	0.1410	0.0833
	Standard Error	0.0588	0.0500	0.0000	0.0366	0.0307	0.0397	0.0403
	Sample Size	6	8	11	18	46	25	7
3 - 4	Sample Proportion	0.0000	0.0000	0.0000	0.0000	0.0870	0.1200	0.1429
	Standard Error	0.0000	0.0000	0.0000	0.0000	0.0420	0.0663	0.1429
	Sample Size	20	5	17	33	60	64	39
4 - 5	Sample Proportion	0.0500	0.2000	0.0588	0.0606	0.1333	0.1719	0.1282
	Standard Error	0.0500	0.2000	0.0588	0.0422	0.0443	0.0475	0.0542

Table 9. Summary statistics of the proportion of tagged male chum salmon that were recaptured at the Rampart recapture site, jointly classified by marking stratum and binned categories of holding time in a live-box (Page 2 of 2).

Holding Time (h)	Statistic	Stratum 1	Stratum 2	Stratum 3	Stratum 4	Stratum 5	Stratum 6	Stratum 7
	Sample Size	5	9	12	25	17	36	19
5 - 6	Sample Proportion	0.2000	0.0000	0.0000	0.0400	0.1765	0.1389	0.1579
	Standard Error	0.2000	0.0000	0.0000	0.0400	0.0953	0.0585	0.0859
	Sample Size	0	0	1	0	2	1	0
6 - 7	Sample Proportion			0.0000		0.0000	0.0000	
	Standard Error					0.0000		
	Sample Size	0	0	0	1	1	1	1
7 - 8	Sample Proportion				1.0000	0.0000	0.0000	0.0000
	Standard Error							
	Sample Size	0	0	0	0	0	1	0
8 - 9	Sample Proportion						0.0000	
	Standard Error							
	Sample Size	0	0	0	0	1	0	0
9 - 10	Sample Proportion					0.0000		
	Standard Error							

Table 10. Parameters and inferential statistics of the generalized linear model of the travel time of tagged chum salmon between the Rapids marking site and the Rampart recapture site.

Parameter	Estimate	Standard Error	Chi-square Test Statistic	Degrees Of Freedom	Significance
Intercept - Stratum 1	2.9634	0.4862	37.2	1	< 0.0001
Intercept - Stratum 2	3.0680	0.4292	51.1	1	< 0.0001
Intercept - Stratum 3	5.1275	0.7610	45.4	1	< 0.0001
Intercept - Stratum 4	3.8455	0.2696	203.4	1	< 0.0001
Intercept - Stratum 5	2.3286	0.1019	522.3	1	< 0.0001
Intercept - Stratum 6	1.4223	0.0569	625.3	1	< 0.0001
Intercept - Stratum 7	1.3250	0.0538	607.6	1	< 0.0001
Crowding (fish-h)	0.0017	0.0004	14.7	1	0.0001

Table 11. Results of exact tests of the hypothesis that the proportion of recaptured chum salmon that were initially released from the right bank fish wheel at the Rapids marking site was equal to the proportion of all tagged chum salmon released from that fish wheel, 0.427, by recapture site.

Recapture Location	Sample Size	Proportion	95% C. I. Limits		Significance
			Lower	Upper	
Rampart	431	0.4292	0.3820	0.4775	0.9555
Stevens Village	64	0.3750	0.2570	0.5049	0.4790
Beaver	15	0.4667	0.2127	0.7341	0.9490
Circle	13	0.5385	0.2513	0.8078	0.5885
Canadian Border	73	0.4932	0.3740	0.6128	0.3041

Table 12. Parameters and inferential statistics of generalized linear models of the proportions of the catches at upriver recapture sites consisting of any marked chum salmon, marked chum salmon that were held in a live-box, and marked chum salmon that were not held in a live-box, as a function of distance (km) from the Rapids marking site.

Fish Category	Parameter	Estimate	Standard Error	Chi-square Test Statistic	Degrees Of Freedom	Significance
All	Intercept	-3.3720	0.0503	4491.5	1	< 0.0001
	Distance	-10.2187	1.5681	42.5	1	< 0.0001
Held	Intercept	-3.8484	0.0645	3556.2	1	< 0.0001
	Distance	-15.3064	2.3228	43.4	1	< 0.0001
Not Held	Intercept	-4.3888	0.0809	2942.1	1	< 0.0001
	Distance	-7.0275	2.3342	9.1	1	0.0026

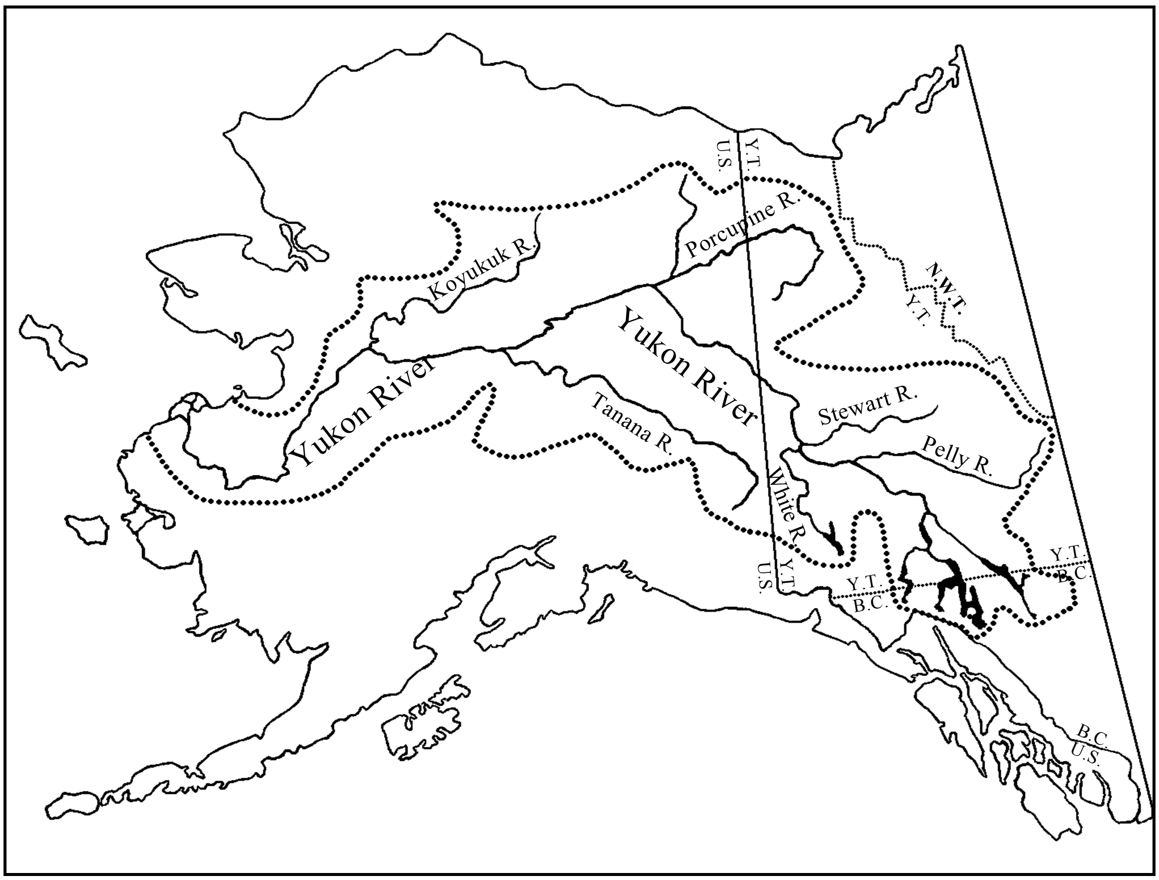

Figure 1. Map of the Yukon River drainage in Canada and Alaska.

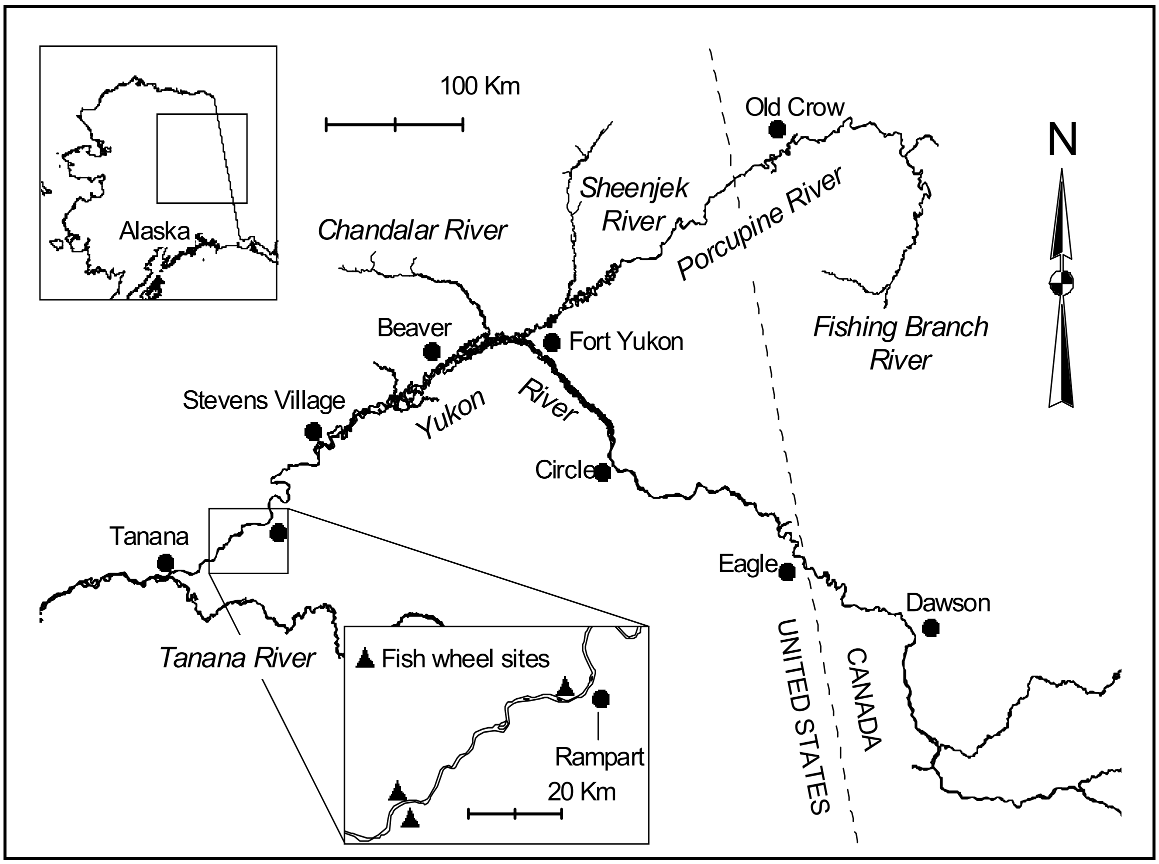

Figure 2. Map of the mark-recapture study site within the Yukon River drainage.

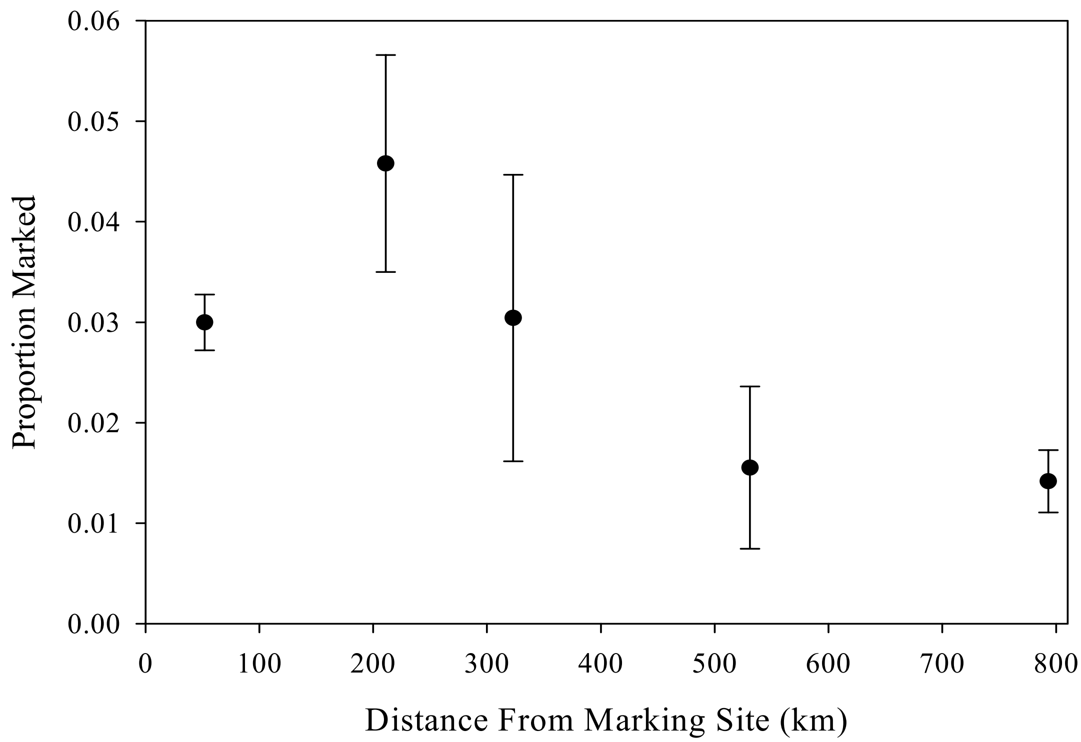

Figure 3. Mark rates observed in the recapture fish wheel catches, with 95% confidence intervals.

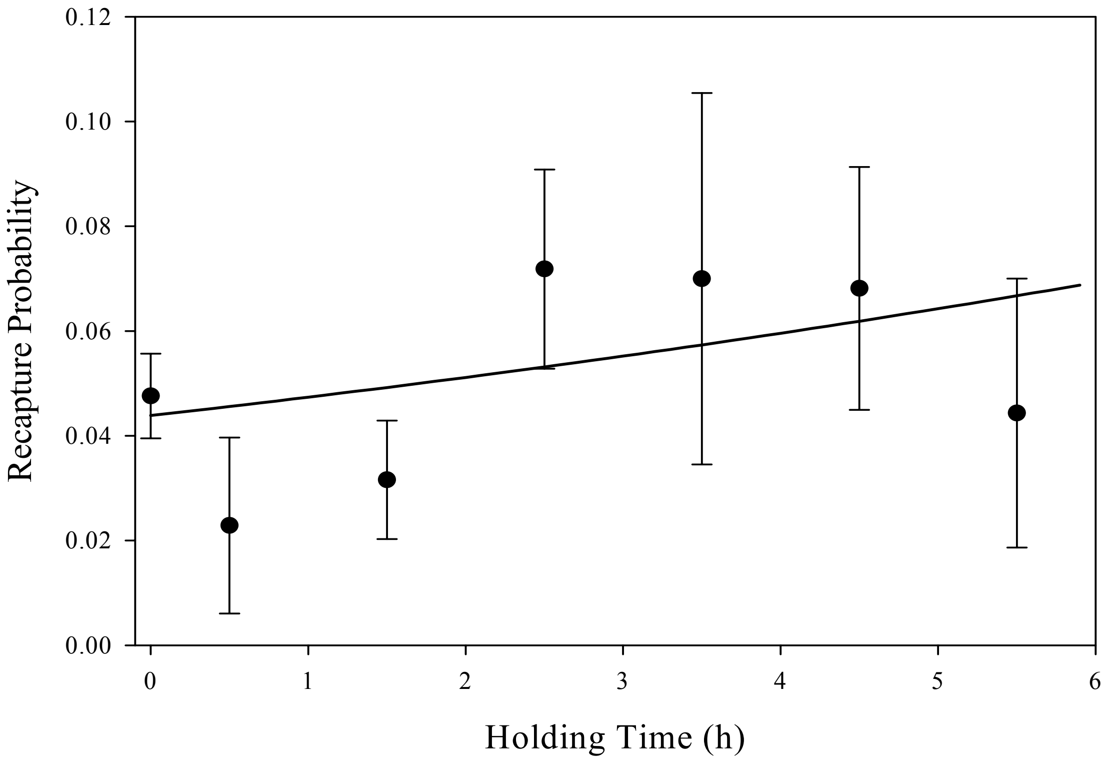

Figure 4. Model of the probability a tagged chum salmon is recaptured at the Rapids marking site, contrasted with the observed proportions recaptured and 95% confidence intervals, as a function of binned holding time categories.

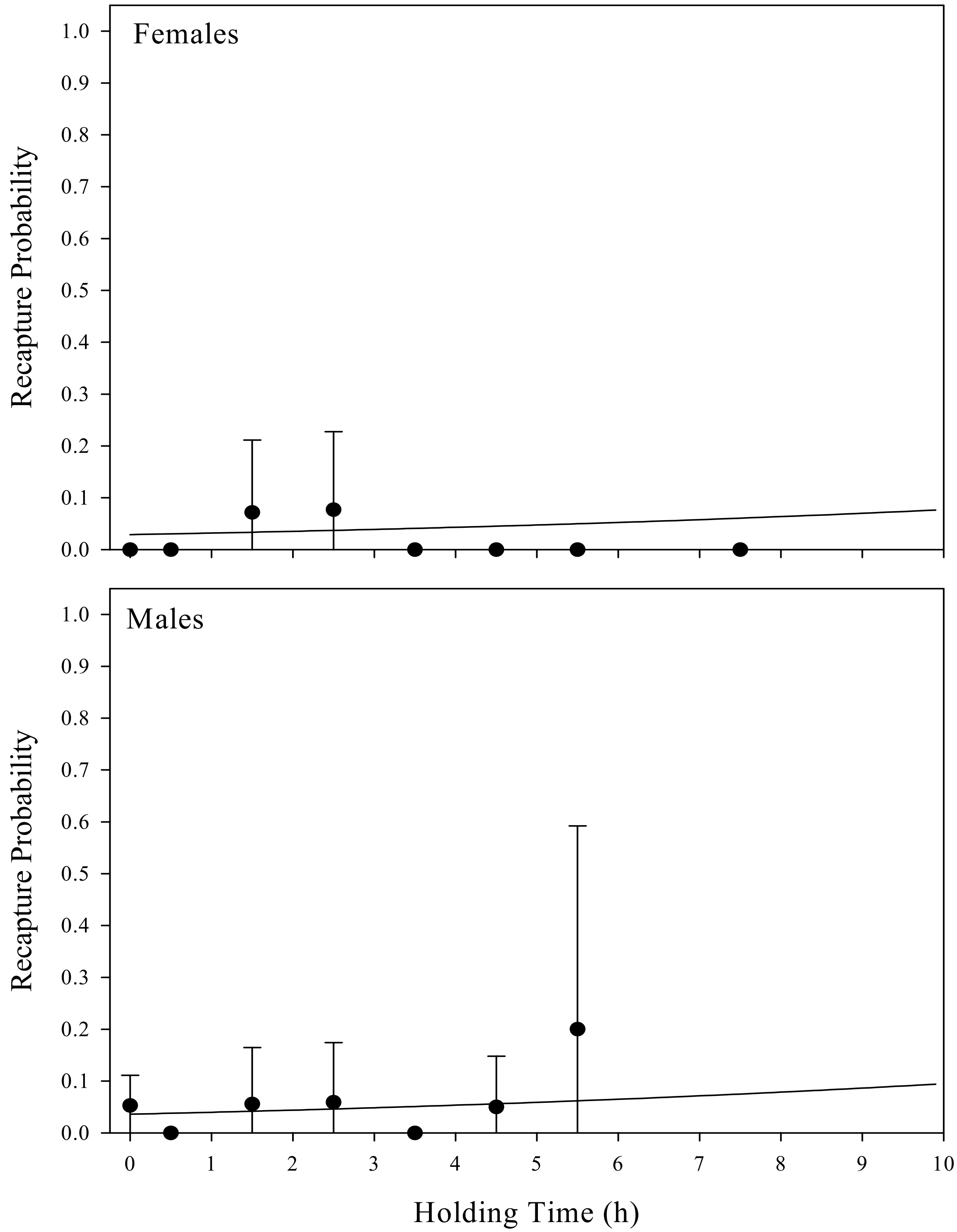

Figure 5. Model of the probability a tagged chum salmon is captured in the Rampart recapture fish wheel, contrasted with sex-specific recapture proportions and 95% confidence intervals, as a function of binned holding time categories for Marking Stratum 1.

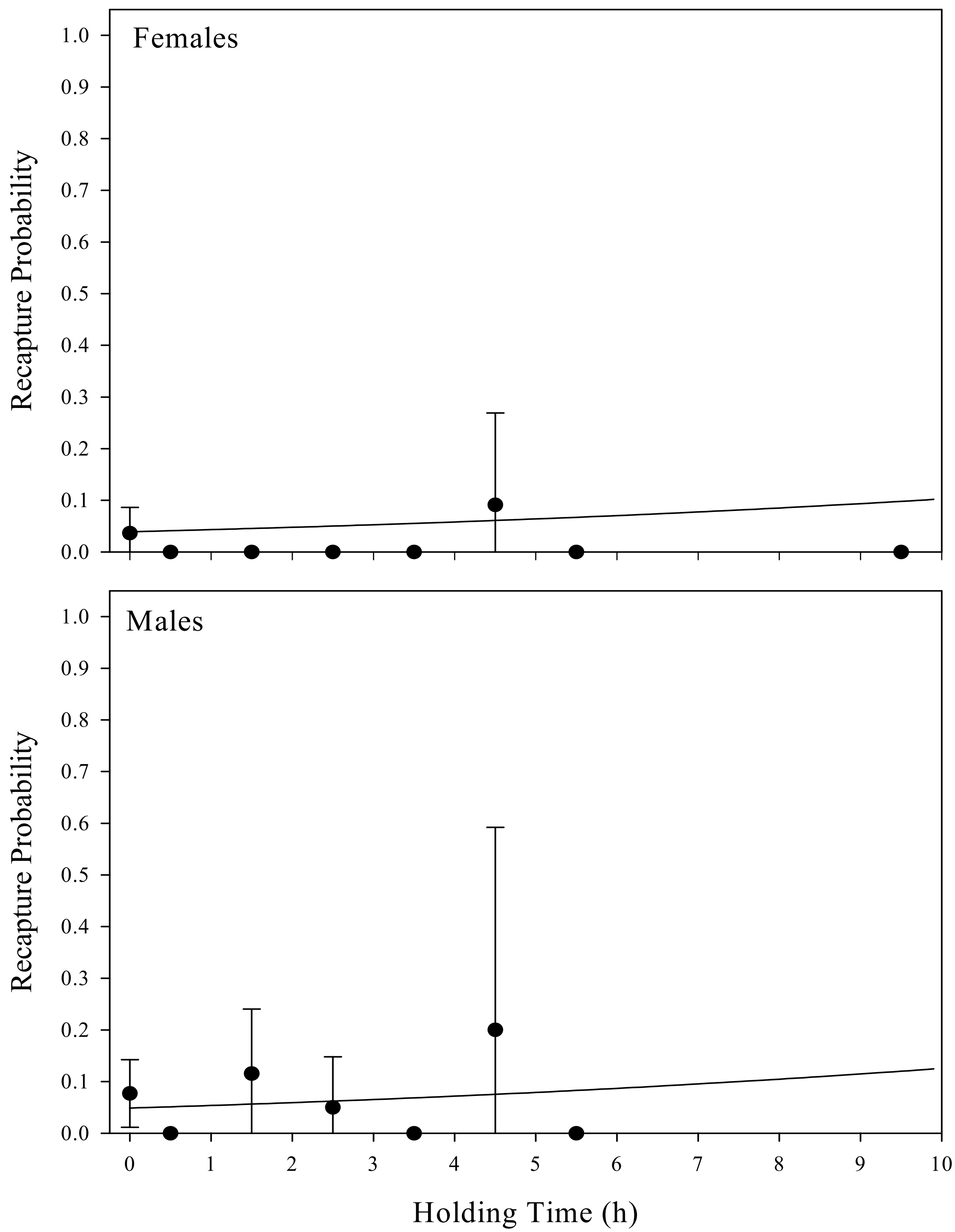

Figure 6. Model of the probability a tagged chum salmon is captured in the Rampart recapture fish wheel, contrasted with sex-specific recapture proportions and 95% confidence intervals, as a function of binned holding time categories for Marking Stratum 2.

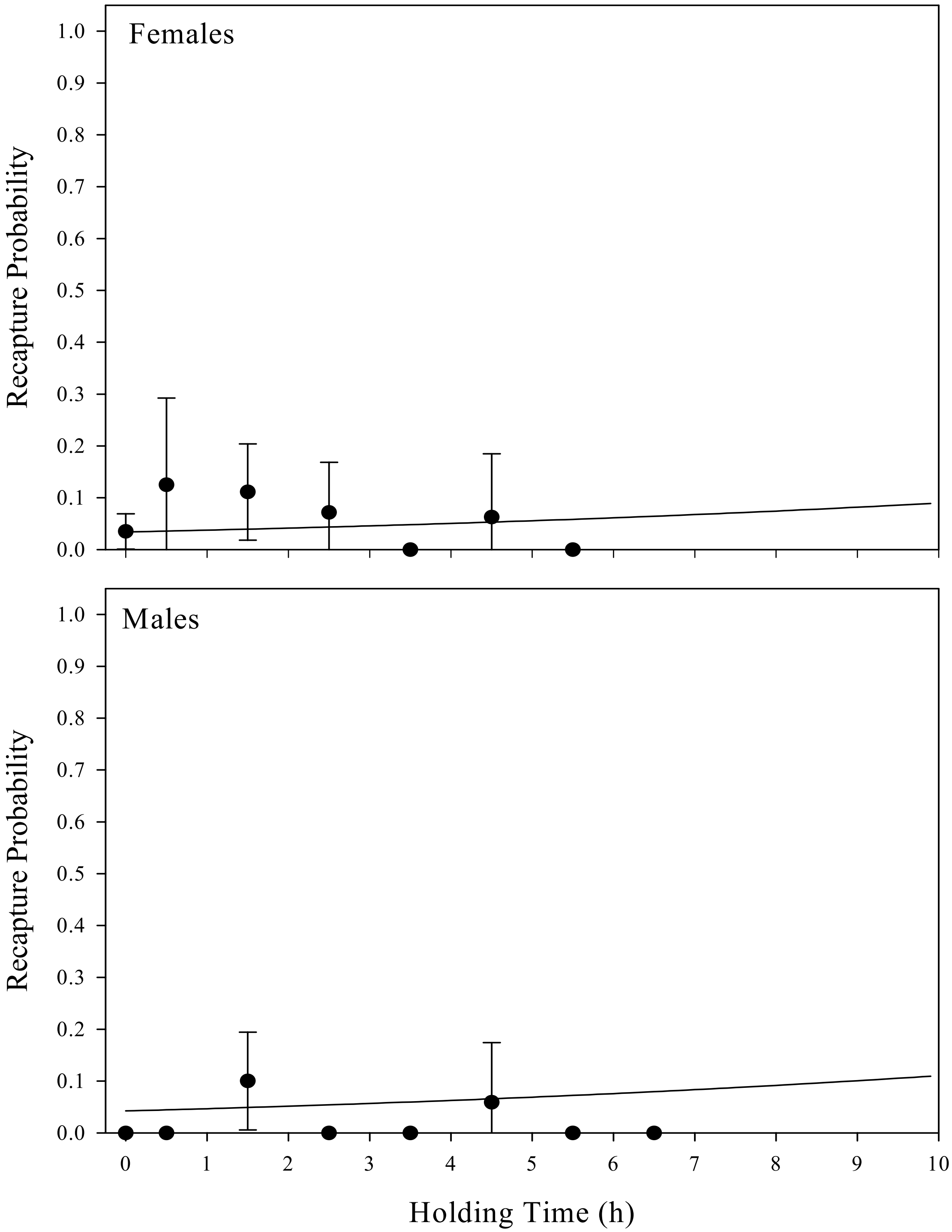

Figure 7. Model of the probability a tagged chum salmon is captured in the Rampart recapture fish wheel, contrasted with sex-specific recapture proportions and 95% confidence intervals, as a function of binned holding time categories for Marking Stratum 3.

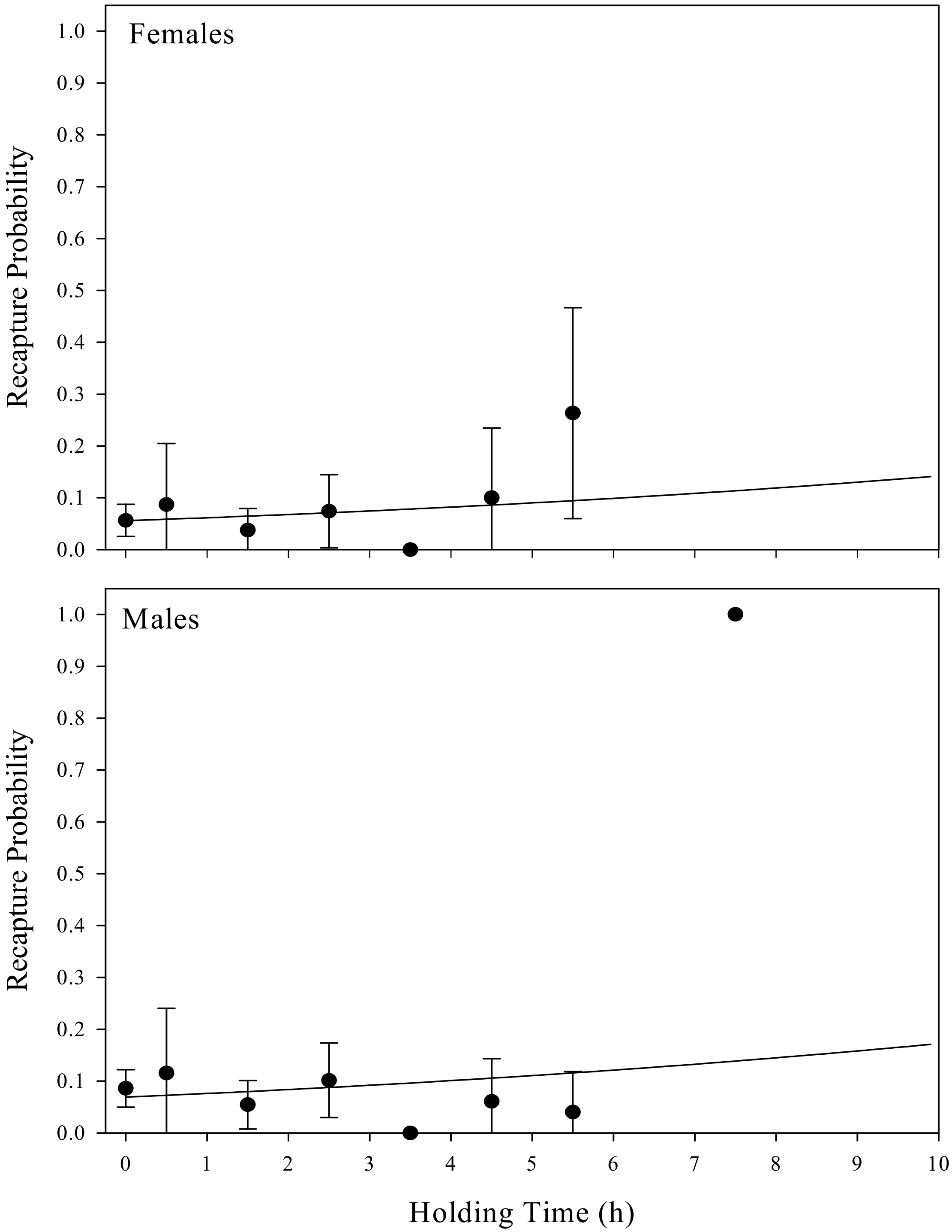

Figure 8. Model of the probability a tagged chum salmon is captured in the Rampart recapture fish wheel, contrasted with sex-specific recapture proportions and 95% confidence intervals, as a function of binned holding time categories for Marking Stratum 4.

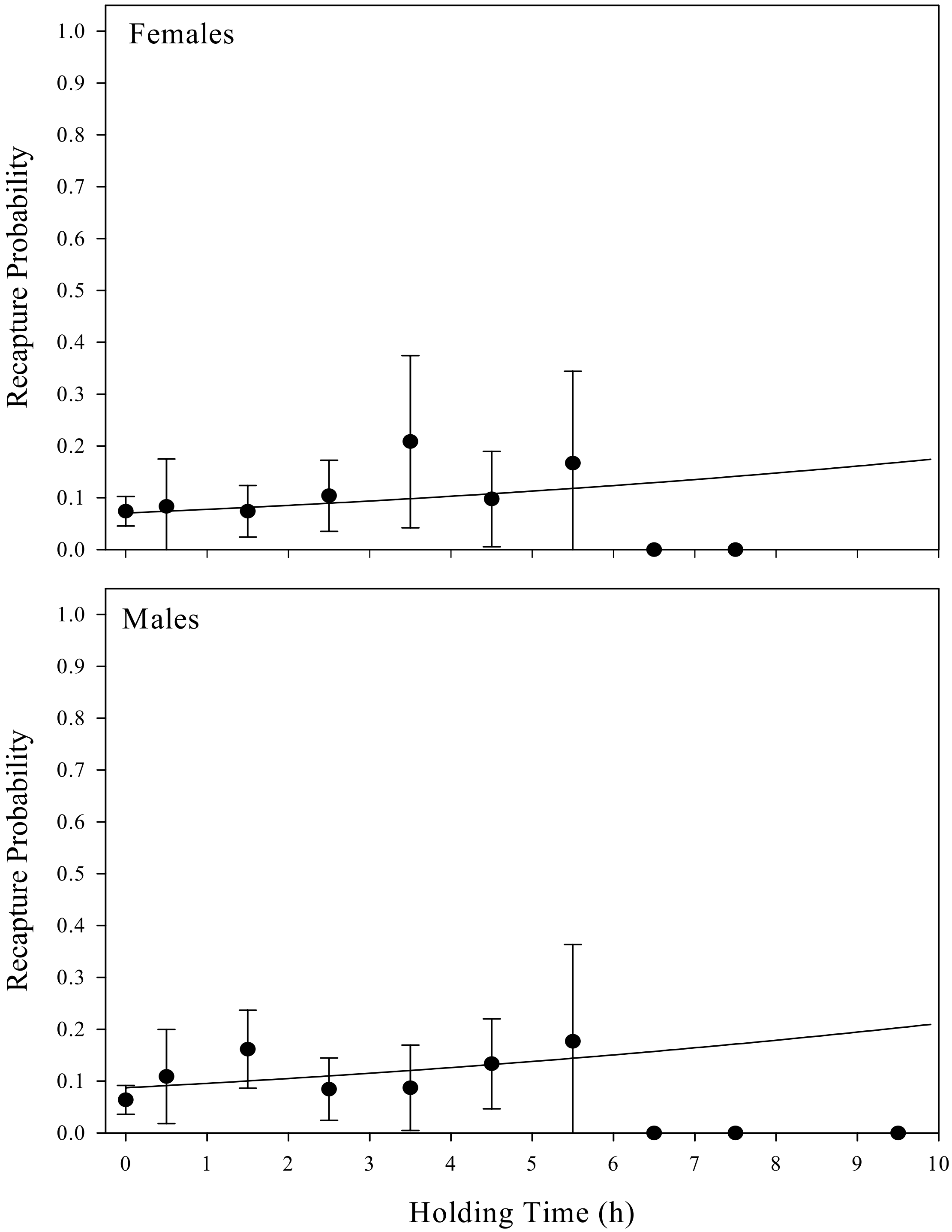

Figure 9. Model of the probability a tagged chum salmon is captured in the Rampart recapture fish wheel, contrasted with sex-specific recapture proportions and 95% confidence intervals, as a function of binned holding time categories for Marking Stratum 5.

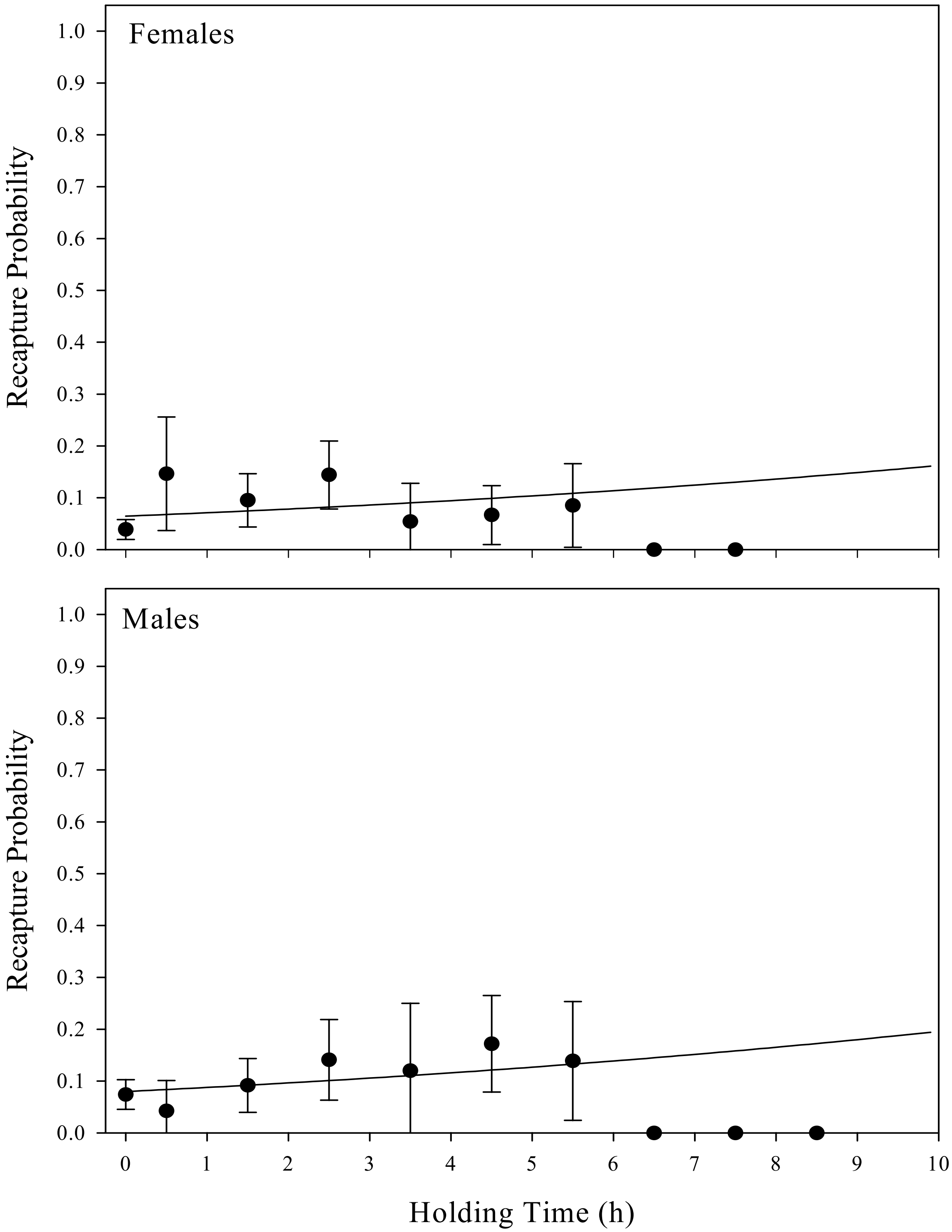

Figure 10. Model of the probability a tagged chum salmon is captured in the Rampart recapture fish wheel, contrasted with sex-specific recapture proportions and 95% confidence intervals, as a function of binned holding time categories for Marking Stratum 6.

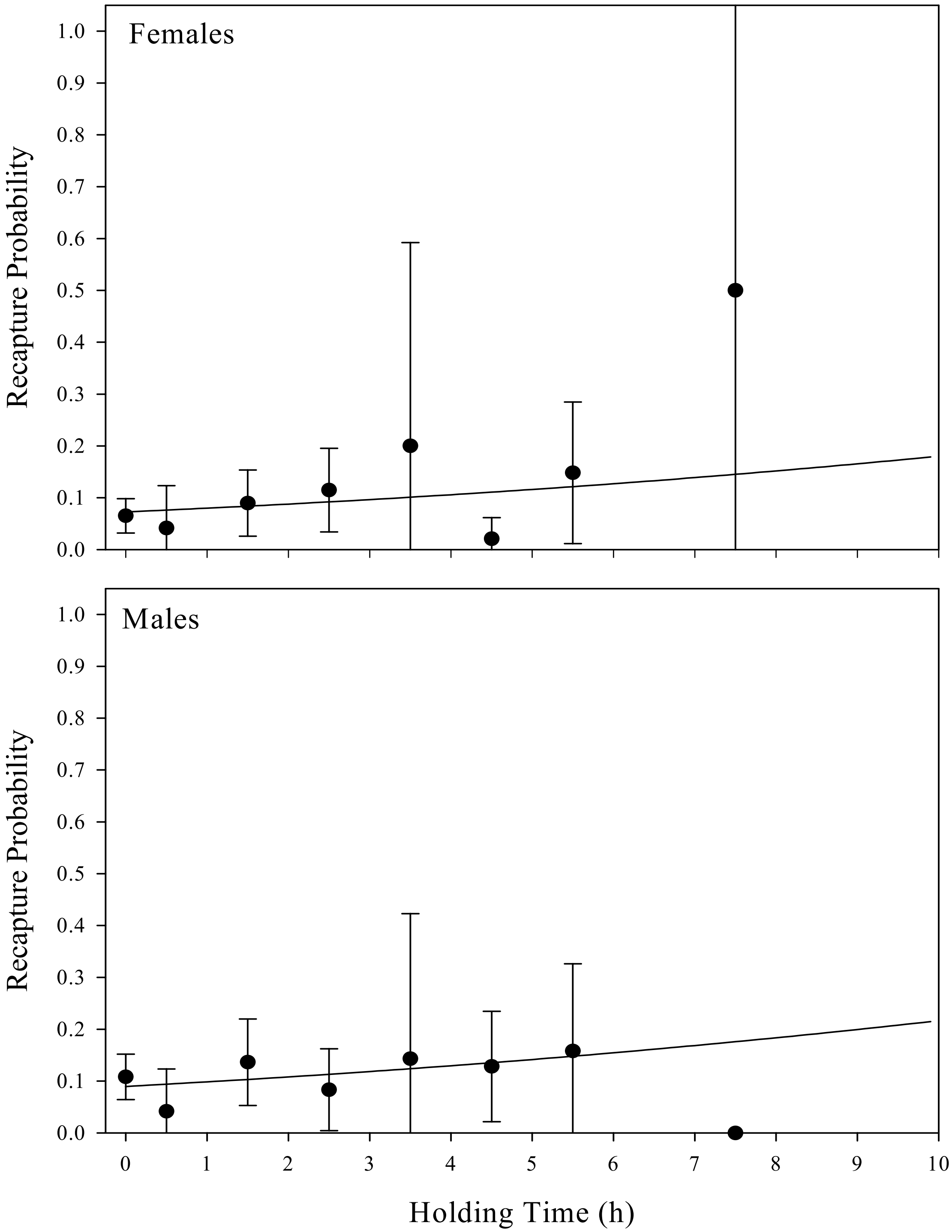

Figure 11. Model of the probability a tagged chum salmon is captured in the Rampart recapture fish wheel, contrasted with sex-specific recapture proportions and 95% confidence intervals, as a function of binned holding time categories for Marking Stratum 7.

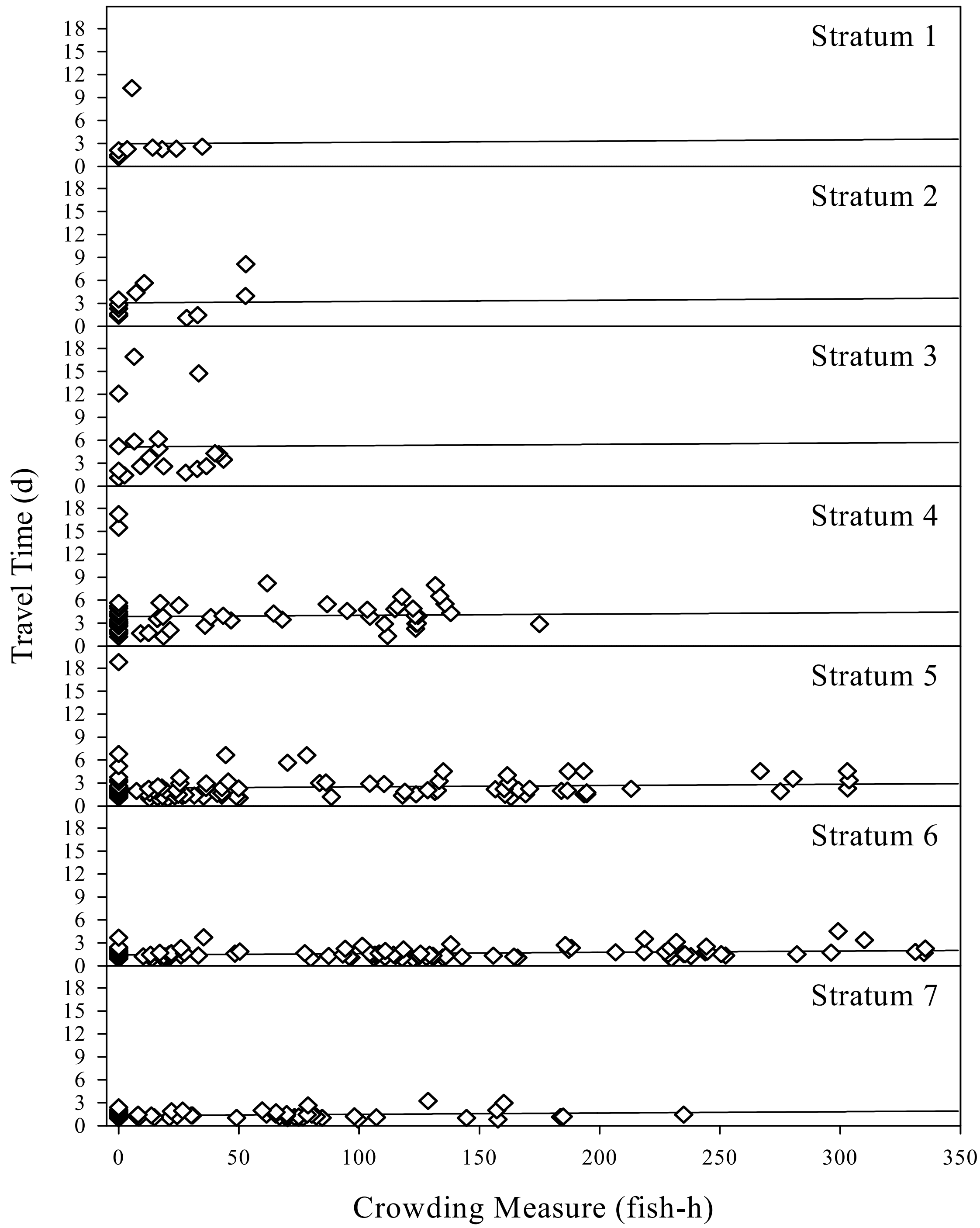

Figure 12. Model and observed data of the travel time between the Rapids marking site and the Rampart recapture site.

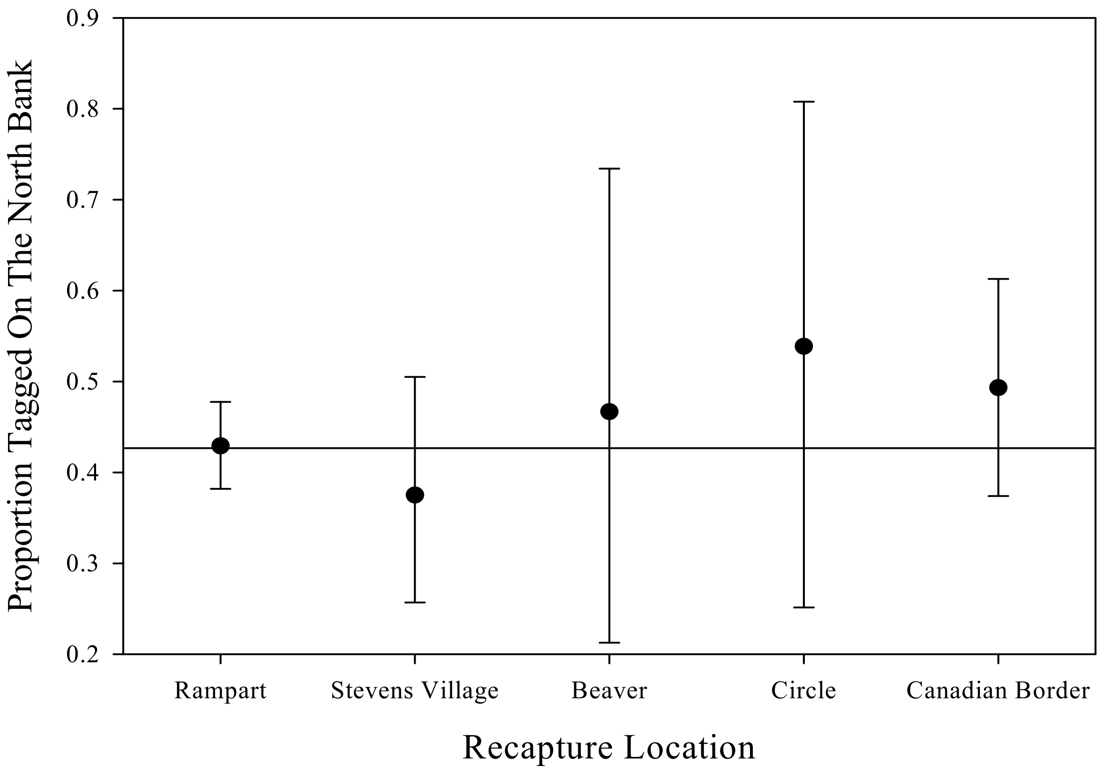

Figure 13. The proportion of recaptured chum salmon that were initially tagged at the right bank fish wheel at the Rapids marking site, with an exact 95% confidence interval, by recapture location.

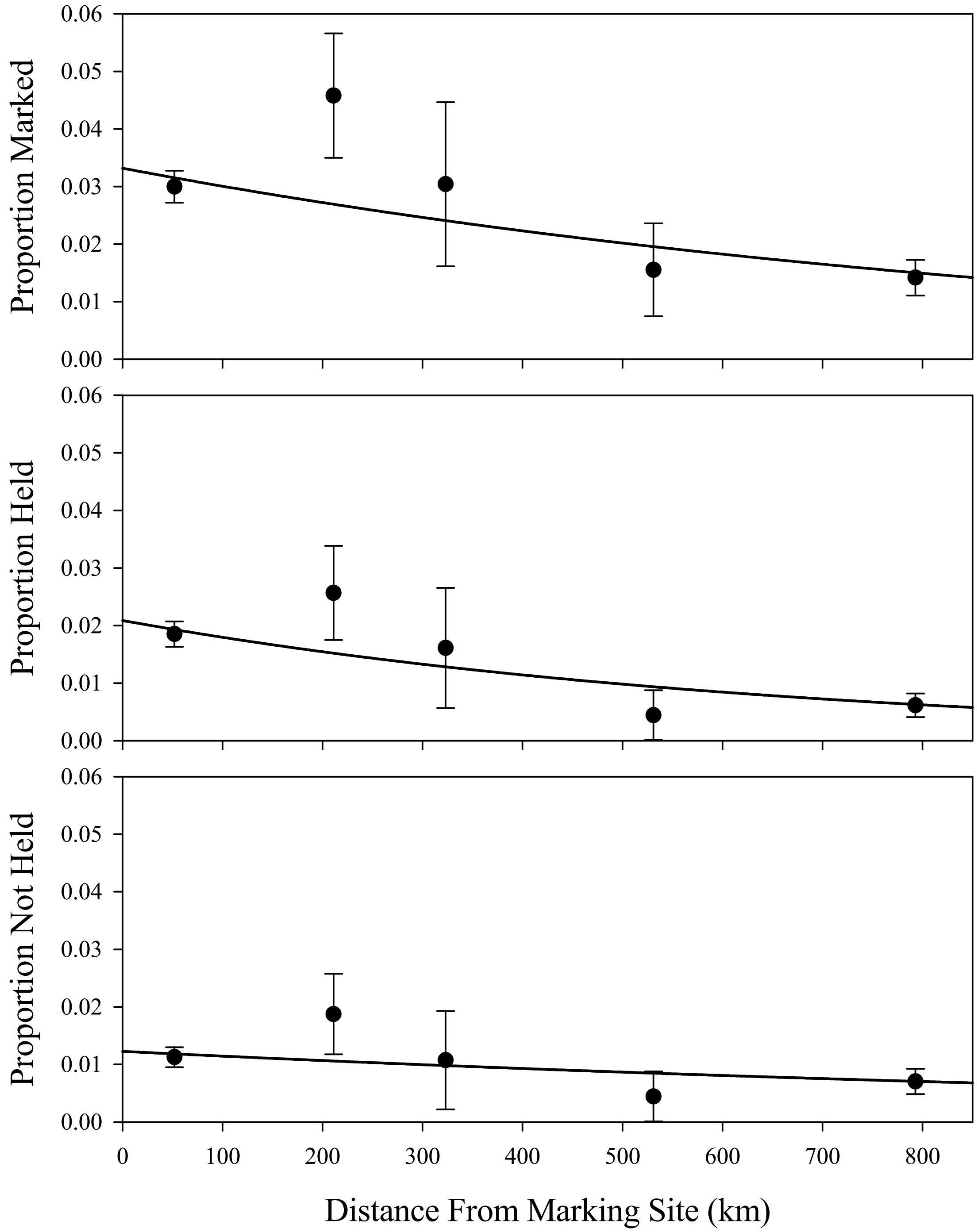

Figure 14. Proportions of all chum salmon that were marked, that were marked and held, and that were marked but not held, with 95% confidence intervals and estimated generalized linear models with distance from the marking site as an explanatory variable.

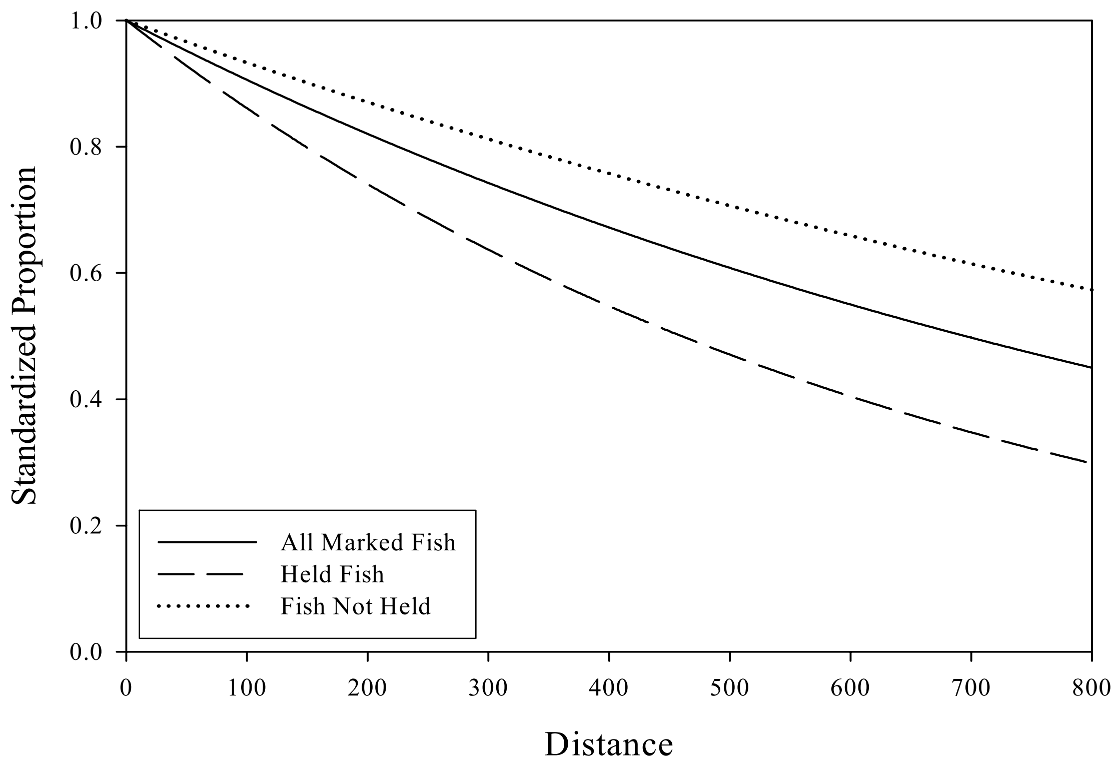

Figure 15. Standardized generalized linear models of the proportions of all chum salmon that were marked, that were marked and held, and that were marked but not held with distance from the marking site as an explanatory variable.