Evidence of Residual Effects From Tagging Yukon River Fall Chum Salmon in 2001

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by

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Abstract

In 2001, the U. S. Fish and Wildlife Service initiated a study of the effects of capturing Yukon River fall chum salmon (*Oncorhynchus keta*) in fish wheels and marking them with spaghetti tags. Two fish wheels were used to capture 8,490 fall chum salmon in the Yukon River main-stem approximately 50 km upriver of the Tanana River confluence. Fish were captured, tagged, and either released immediately or held for as long as 5.8 h in a live-box, a submerged holding pen attached to the side of a fish wheel. Fish were recaptured in fish wheels at four upriver sites, near Rampart, Beaver, and Circle, Alaska and near the international border in Canada. Fish that were held in a live-box for longer periods of time had a higher probability of recapture in the marking fish wheels, traveled more slowly between the marking site and the Rampart recapture site, and had a higher probability of recapture at the Rampart site. Conversely, increased holding time in a live-box was associated with a reduced probability of recapture at the more distant Beaver, Circle, and Canadian locations. Mark rates, i.e., the proportion of a catch bearing marks, of 4.2%, 2.4%, 1.8%, and 1.6% were observed at the four upriver locations, respectively. The decline in mark rates with increasing distance from the marking site was observed in both immediately released and held fish. Although the decline appeared somewhat more severe for fish that were held in a live-box, the difference was not statistically significant. Holding fall chum salmon in a live-box appears to negatively affect their ability to migrate, but does not fully explain the reduced mark rates observed at upriver locations. The primary cause of the decline in mark rates remains unknown.

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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, the northern-most extension of the Rocky Mountains, 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 enter the river in June and July and spawn in tributaries of the lower and middle portion of the main-stem. Fall chum salmon 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 when both commercial and subsistence fisheries were restricted or closed. The primary goal of salmon management on the Yukon River is to maintain the abundance of spawning populations within specified ranges in selected spawning locations throughout the drainage (Vania et al. 2002). Because most fisheries occur large distances from the spawning grounds, the ability of management to achieve the spawning goals is greatly increased by the availability of in-season estimates of abundance in 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 main-stem 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 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 main-stem 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 abundance in-season and harvest fall chum salmon commensurate with their abundance. 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 status of 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. Further investigations indicated a progressive reduction in mark rates as distance from the tagging site increased. Nine hypotheses that could contribute to the reduction in mark rates were developed and the plausibility of the hypotheses were evaluated using available data (Underwood et al. 2000b, 2000a). Although the data were not conclusive, the hypothesis that the capture or tagging process increases the mortality rate between the recapture site near Rampart, Alaska and upriver locations was thought to be the only potential cause consistent with all available information. 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 consistent with a PTM hypothesis (Underwood et al. 2002, in press.).

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 mark-recapture marking site. The upriver migration of tagged fish was primarily monitored with fixed receiver stations (Eiler 1995), though a small number of aerial surveys was also flown. The results of this study provide mixed support to the PTM hypothesis. In one year, a relatively large number of radio-tagged fish appeared to remain in the Yukon River main-stem or small tributaries not thought to support populations of fall chum salmon. This result is consistent with the PTM hypothesis, though the magnitude of the effect is somewhat less than what would be expected based on the mark-recapture data (Underwood et al. 2000b). In the other year, relatively few fish remained in the same main-stem areas. However, the mark-recapture project documented substantial declines in mark rates in both 1998 (Underwood et al. in press) and 1999 (Tevis Underwood, U. S. Fish and Wildlife Service, unpublished data). The cause of the difference in the telemetry results from 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 mortality is of great 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 10% and 15% at the two sites, respectively (Underwood et al. 2000b). An increase in mortality due to project operations has the potential to affect substantial numbers of fish. 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. One objective of the study was to more rigorously document the reduced mark rates previously observed upriver from the marking site. With the exception of data collected at Canadian research sites, upriver samples for mark rates were not collected throughout the fall chum salmon migration. Because the mark-recapture study design called for a constant number of tagged fish to be released each day (e.g., Underwood et al. 2000b), 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 from these upriver sources was expected to more conclusively document mark rates.

A second study objective 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. Prior to 2001, sampling protocols of the mark-recapture study were designed only for purposes of abundance estimation (e.g., Underwood et al. in press). 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 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 fish 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 conditions. This component of the study was expected to provide a greater understanding of handling practices that might be associated with decreased recapture rates so that such practices might be avoided in future studies.

Study Area

The Rampart mark-recapture experiment was conducted on the Yukon River main-stem between its confluence with the Tanana River and the village of Rampart, Alaska (Figure 2). The marking site was located approximately 50 km above the Tanana River confluence, in an area known locally as the 'The Rapids'. The river in this area is characterized by a single deep channel and swift current. The recapture site was 52 km upriver near Rampart, Alaska. Two additional recapture fish wheels were operated on the Yukon River main-stem approximately 323 km and 531 km from the marking site, near 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 for our study.

Methods

Rampart Mark-Recapture Study

The core component of this investigation is the traditional Rampart mark-recapture study that has been conducted annually since 1996 (Underwood et al. 2000b). 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 and Bromaghin (2003).

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 300 fish to be tagged daily, except Sundays when no fish were tagged. Fish were captured and processed during four daily work sessions to spread the release of tagged fish throughout the day. 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 approximately half of the left pelvic 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 released were recorded to the nearest 1 min.

Fish capture times were recorded as accurately as possible, given the conditions under which fish were captured and held. The capture times of fish that were taken directly from the chute, tagged, and released without being in the live-box were recorded to the nearest minute. Two protocols were used to record capture times of fish that were held in the live-box. Prior to 24 August, fish that were held in the live-box were removed from the live-box with a dip net, tagged, and released. Capture times for these fish were not known exactly, but were approximated as the midpoint between the time the fish wheel was started and either the time the fish wheel was stopped or the time of removal from the live-box, whichever occurred first. Fish wheel start and stop times were usually reset every 1 h, so capture times were recorded with variable precision that could range from nearly exact to within 0.5 h. A second protocol was initiated on 24 August. During a single work session, fish captured at the first fish wheel visited by the crew were captured from the chute, tagged, and placed into the live-box. When approximately half of the target number of fish for the work session was tagged, the first fish wheel was stopped and the crew would travel to the second fish wheel, where all fish were captured from the chute and released immediately. At the end of the work session, the crew would revisit the first fish wheel and simultaneously release all fish being held in the live-box. The first wheel to be visited was alternated between work sessions within a day and between the first work session of consecutive days in an attempt to avoid potential 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 operated 24 hours each day, seven days a week. Crews tended the fish wheel from approximately 0500 hours to 2300 hours each day, 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. Capture times for fish captured from the chute were recorded in the data logger using its internal clock. For fish removed from the live-box, the time of capture was approximated as the midpoint between the time the fish wheel was started 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, so capture times 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 recaptured fish, and any incidence of tag loss were recorded.

Upriver Fish Wheel Operations

Operational plans for the recapture fish wheels near Beaver and Circle, Alaska (Figure 2) called for the wheels to fish for a minimum of 6 h on each of five days per week. The fish wheel contractors were to keep the wheels operating efficiently and monitor the fish wheels when they were being operated. 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. 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 (e.g., Johnson et al. 2002) also served as recapture fish wheels for our study. The fish wheels were located approximately 8 km apart on the right bank of the Yukon River main-stem 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 were serviced. Fish were captured and held in live-boxes, from which they were removed, tagged, and released during three daily tagging sessions. Canadian biologists were aware of our study and concern over the potential for mortality or tag loss, and kindly agreed to examine fish for the presence of our 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. In addition, 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 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. 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. Marking stratum was utilized as a categorical nuisance parameter to coarsely adjust for possible temporal changes in factors such as water velocity or fish wheel efficiency, essentially including a base recapture rate 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 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. Failure to evaluate model fit can lead to unnecessarily complicated models, or poorly-founded conclusions derived from poorly-fitting models. 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 actual features of the data. In some cases, additional statistical tests, such as Smirnov tests (Hollander and Wolfe 1999) or chi-square tests (Agresti 2002), were conducted, as appropriate under the circumstances of each individual model, to assist in model evaluation.

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 (e.g., Underwood and Bromaghin 2003). Additional insight into mixing might be obtained by comparing the bank at which fish were initially tagged for those fish recaptured at particular locations. Such an analysis, for example, could reveal that certain fish 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 one of the four recapture sites. 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 that were tagged at that fish wheel was tested using an exact binomial test (Agresti 2002, Hollander and Wolfe 1999). A separate, identical, hypothesis was tested for fish recaptured at each of the four recapture locations. Fish that escaped before their tag number could be determined were excluded from the analysis.

Results

Catch Statistics

Fish wheels at the marking site operated from 30 July to 15 September, releasing 8,490 tagged fall chum salmon. The data records of 13 of these fish were incomplete, so analyses were based on data from 8,477 fish. The recapture fish wheel at Rampart caught 11,814 fish from 31 July to 18 September, 501 of which were recaptures. The Beaver recapture fish wheel captured 807 fall chum salmon, 19 of which were tagged, from 12 August through 26 September, 2001. Two of the tagged fish captured in the Beaver fish wheel were retained during open periods of the subsistence fishery. The Circle recapture fish wheel operated from 13 August through 29 September, catching 2,387 fish, 42 of which were tagged. Although some tagged fish were retained in the subsistence harvest from the Circle fish wheel, the exact number is not known because tag numbers of retained fish were not always recorded. The Canadian fish wheels captured 3,277 fall chum salmon, 51 of which were marked, from 2 August to 4 October, 2001 (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 release at the four recapture sites are presented in the table. Capture histories of individual fish with complete data are summarized in Table 2.

No tag loss was observed at the Rampart, Beaver, or Circle fish wheels. The Canadian fish wheel crew began examining every fish captured for secondary marks on 30 August, 2001 (Pat Milligan, Fisheries and Oceans Canada, personal communication). No tag loss was observed among 2,905 fall chum salmon examined after that date. Fish captured prior to 30

August were tagged as part of the Canadian mark-recapture study, and tag-induced injuries likely would have been noticed, but the fish were not explicitly examined for the presence of a secondary mark.

Forty-eight percent of the marked fish were released from the fish wheel on the right (north) bank of the river. Females constituted 55% of the tagged fish released from the marking site. Female lengths ranged from 47 cm to 68 cm, while male lengths ranged from 48 cm to 72 cm. Live-box holding times ranged from 0.0 to 5.8 h, with an average of 0.7 h. Twenty nine percent of the tagged fish were released without being held. The average measure of crowding in the live-box was 18.7 fish-h, ranging from 0.0 for fish that were not held to a maximum of 199.2 fish-h. Individual fall chum salmon were captured from one to four times in the two marking fish wheels (Table 2).

Mark rates observed at each recapture site, computed using only the first recapture of tagged fish caught more than once at a single location, are plotted versus distance from the marking fish wheel in Figure 3. Point estimates decreased nearly 50% between Rampart and Beaver, and declined more gradually further upriver. The pattern and magnitude of the decline in mark rates is similar to that observed in past years (Underwood et al. in press).

Analysis of Data From the Marking Site

For the 515 marked fish recaptured at the marking site (Table 2), the first recapture of each fish was identified and the probability of recapture 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 an intercept for each marking stratum, terms for sex, length, holding time, and crowding, as well as two interaction terms, i.e.,

$$E\left[\log\left(\frac{p_{Mi}}{1-p_{Mi}}\right)\right] = \beta_{0i} + \beta_1 S + \beta_2 L + \beta_3 H + \beta_4 C + \beta_5 SL + \beta_6 HC, \qquad (1)$$

where

where	p_{Mi}	=	the probability of recapture at the marking site 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 sex, female = 1 and male = 0,
	β_2	=	length parameter,
	L	=	length,
	β_3	=	holding time parameter,
	H	=	holding time,

β_4	=	crowding parameter,
C	=	measure of crowding,
β_5	=	parameter for the interaction of sex and length,
β_6	=	parameter for the interaction of holding time and the measure of crowding, and

E[x] denotes the mathematical expectation of x. Estimation of the model parameters is summarized in Table 3.

The evaluation of model fit and interpretation of individual terms is complicated by the significant interactions, and a meaningful method of graphically comparing the model and the data wasn't apparent. For that reason, an exact chi-square test (Agresti 2002) of the 2-by-2 contingency table formed by indicator variables of whether or not fish were held and fish were recaptured was conducted. Of 6,000 fish that were held, 7.40% were recaptured at least once. Only 2.91% of the 2,477 fish that were not held were recaptured. The test was significant (χ^2 = 61.92, df = 1, $P_\alpha < 0.0001$), which indicates the model may well be detecting meaningful characteristics of the data, even though the complexity of the model may be suspect.

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 in the data, lack of structure in the data, or that the assumed inverse gaussian distribution wasn't able to adequately fit the structure of the data. Attempts to fit models using a gamma distribution were equally unsuccessful. No further analysis of these data was attempted.

Analysis of Data From the Rampart Recapture Site

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

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

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	=	holding time parameter, and
	H	=	holding time.

Estimation of the model parameters is summarized in Table 4. 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. Sample sizes, observed proportions, and binomial standard errors are presented in Table 5. Observed proportions and normal-approximation 95% confidence limits are compared to the final generalized linear model in Figure 4. There is a clear tendency for recapture rates to increase with holding time in both the observed data and the estimated model, which lends credibility to the model.

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. During model development, a significant interaction between holding time and the number of times fish were captured was encountered ($\chi^2 = 9.65$, df = 1, $P_\alpha = 0.0019$). The model indicated that the travel time of fish caught once increased with holding time, while the travel time of fish caught more than once had decreased as holding time increased. An attempt was made to verify the practical significance of the interaction by comparing plots of the model and the data. As an example, the plot for one of the seven marking strata is presented in Figure 5. No practical explanation for the differences between the four subplots was apparent, relatively few fish were captured more than once, and the major differences among the subplots occurred in regions of low data density. For those reasons, we concluded that the interaction was spurious, removed the interaction term from the model, and proceeded with model development as if the term had not been significant.

The final model contained an intercept for each marking stratum and terms for sex, length, and holding time in the live-box, i.e.,

$$E\left[T_i\right] = \beta_{0i} + \beta_1 S + \beta_2 L + \beta_3 H \ , \qquad (3)$$

where
T_i = the travel time of fish released in marking stratum i,
β_{0i} = intercept parameter for fish released in marking stratum i,
β_1 = sex parameter,
S = indicator of sex, female = 1 and male = 0,
β_2 = length parameter,
L = length
β_3 = holding time parameter, and
H = holding time.

Parameter estimates for the sex, length, and holding time parameters were all positive (Table 6), indicating that mean travel times were greater for females, for longer fish, and for fish held longer in the live-box. The estimated model for the mean travel time is plotted with the observed data, by stratum, in Figure 6 through Figure 12.

The apparent effect of holding fish on the probability of recapture at Rampart has the potential to negatively bias the mark-recapture abundance estimate. For this reason, we attempted to estimate abundance, based on the methods of Underwood and Bromaghin (2003), using only those fish that were not held. However, because of the greatly reduced sample size and the sparsity of the movement-recapture matrix of the Darroch (1961) estimator, we were unable to obtain an estimate based on the seven strata used by Underwood and Bromaghin (2003). After pooling data from Strata 1-2, Strata 3-4, and Strata 5-7, we obtained an estimate of 295,780, with a standard error of 62,832. Underwood and Bromaghin (2003) reported a fall chum salmon abundance estimate of 201,766 fish, with a standard error of 9,578. Given the large estimated standard error of the estimate based on data from fish that were not held, the two point estimates are not statistically different.

Analysis of Data From Upriver Recapture Sites

Relatively few fish were recaptured in the Beaver, Circle, or Canadian recapture fish wheels, so the only analyses performed on the individual data sets was the computation of mark rates (Figure 3). For other analyses, data from all three recapture locations were pooled to form a single recapture event referred to as the ‘upriver recapture site’.

The relatively small number of recaptures in the upriver fish wheels precluded use of models with high-order interactions; in general, such models failed to converge. For that reason, model building efforts for the probability of recapture began with a model containing an intercept term for each marking stratum, terms for fish sex, fish length, holding time in the live-box, crowding in the live-box, the number of times fish were captured at the marking site, the number of times fish were captured at the Rampart recapture site, and all two-way interactions of these factors. The final model contained a single intercept term and a term for holding time, i.e.,

$$E\left[\log\left(\frac{p_U}{1-p_U}\right)\right] = \beta_0 + \beta_1 H, \qquad (4)$$

where p_U = the probability of recapture in the upriver fish wheels,
β_0 = intercept parameter,
β_1 = holding time parameter, and
H = holding time.

Parameter estimates and inferential statistics are presented in Table 7. The holding-time parameter is significantly less than zero, reflecting the finding that increased holding time is associated with a reduced probability of recapture in the upriver fish wheels. The estimated model is plotted in Figure 13. An evaluation of the fit of the model to the data is hampered by the relatively small number of recaptures, which precludes meaningful binning of holding time. As a surrogate, a Smirnov test (Hollander and Wolfe 1999) of the equality of the distributions of holding time for fish that were (n = 110) and were not (n = 8367) recaptured in the upriver fish wheels was performed. The test results suggest that the distributions are not equivalent (D = 0.2060, $P_\alpha < 0.0001$; Figure 14). The fish that were recaptured upriver tended to have shorter holding times than those that were not recaptured, suggesting that the generalized linear model detected meaningful characteristics of the data.

Of the 8,490 fish tagged at the marking site, 4,084 (48%) were tagged at the right-bank fish wheel. For the fish recaptured at each of the four recapture sites, the hypothesis that 48% of them had been tagged at the right-bank fish wheel was tested using an exact binomial test, as previously described. The test results for fish caught at Rampart (n = 489, z = -0.1094, $P_\alpha = 0.9493$), Circle (n = 42, z = -0.0624, $P_\alpha = 1.0000$), and Canada (n = 48, z = 0.5523, $P_\alpha = 0.6827$) suggest the proportions did not differ significantly from the overall proportion of 0.48. However, the results of the test for fish recaptured at Beaver were statistically significant (n = 18, z = 2.5201, $P_\alpha = 0.0204$). The observed proportions and exact 95% confidence limits are presented in Figure 15.

Travel Times

Summary statistics of the travel times of tagged fall chum salmon between the marking site and upriver locations were computed (Table 8). No further analysis of these data was performed because of the relatively small sample sizes.

Evaluating the Effects of Holding Fish

The models previously summarized suggest that holding fish in a live-box negatively affects both recapture rate and travel time. However, that doesn't necessarily imply that holding fish alone is associated with the reduced mark rates observed at upriver sites. To investigate that possibility, the fish recaptured at all four recapture sites were classified as not held in a live-box at the marking site, held for any length of time, and held for at least 0.5 h; note that the two classifications of holding time are not exclusive. The proportions of the total catch at each recapture site comprised of fish in these three categories of holding time were computed. Generalized linear models were used to model the number in each category, as a binomial random variable using a logit link, as a function of distance from the marking site. The results of fitting a separate model to each of the three sets of proportions are presented in Table 9. To facilitate a comparison of the models, they were standardized so that the predicted proportions were 1.0 at a distance of zero (Figure 16). The estimated distance parameters of the three models are not statistically different (Table 9), though there appears to be a tendency for holding time to increase the decline of the mark rates.

Discussion

The results of this study conclusively document that holding fish in a live-box at the Rapids marking site negatively impacts their subsequent upriver migration. Held fish were more likely to be recaptured at the marking site (Table 3), took longer to migrate to the Rampart recapture site (Table 6, Figures 6-12), and had an increased probability of capture at that site (Tables 4-5, Figure 4). We conjecture that holding fish elicits a stress response (e.g., Clements et al. 2002), and increases the tendency of fish to travel near the river bank and be captured in the Rampart fish wheel.

This finding has implications for the use of live-boxes in fishery management. In the Yukon River drainage, 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 was manned, 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 these results imply that live-boxes may not be as innocuous as was previously thought. However, subsistence fishers that use fish wheels have not commonly adopted use of live-boxes (Bonnie Borba, Alaska Department of Fish and Game, personal communication).

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; Underwood and Bromaghin 2003; Cleary and Hamazaki 2002; Ericksen 2002; and Johnson et al. 2002). If the use of live-boxes was generally found to negatively affect fish, the cost to research programs in terms of reduced sample sizes or increased personnel costs to actively monitor fish wheels could be substantial. However, other researchers that have investigated the effects of holding fish have not obtained similar findings. Kerkvliet and Hamazaki (2003) did not observe differences among coho salmon held for different lengths of time. Cleary and Hamazaki (2002) found that chum salmon with longer mean holding times sometimes had elevated migration rates. The cause of the differences among these findings is unknown. It is possible that the greater sample sizes in our study, or the increased precision with which holding time was measured, made the effect more discernable. It is also possible that some unidentified characteristic of our study that is correlated with holding time, is impacting the fish we are studying.

The elevated capture probability of held fish at the Rampart recapture site has implications for the annual mark-recapture study. This is effectively a 'trap-happy' response (Seber 1982), and negatively biases abundance estimates. Some fish have been held at the marking site in every year of the study, though steps have been taken to reduce holding times in recent years (Underwood et al. 2000b). Underwood et al. (2000b) reported that abundance estimates are less than run reconstructions based on all available upriver data sources in three of four 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 2001, the estimate of abundance increased by nearly 50% when data on held fish were excluded. However, the number of marked fish was greatly reduced, the original seven strata had to be pooled into three strata, and the standard error of the estimate increased by over 650%. For these reasons, although the point estimate was expected to increase, the magnitude of the increase must be viewed with caution.

The decline in mark rates at upriver locations observed in this study is consistent with observations made in prior years (Underwood et al. 2000a, 2002, in press). The collection of data throughout the duration of the 2001 migration serves to affirm the data collected under less rigorous protocols in prior years and increases the confidence one may place in the earlier results. The decline in mark rates is substantial, with an estimated decrease of approximately 50% occurring between the Rampart and Beaver recapture sites in 2001 (Figure 3). Three factors have the greatest potential of producing a decline of that magnitude: tag loss, incomplete mixing of marked and unmarked fish between the marking and Rampart recapture sites, 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. In 2001, as in some prior years (Underwood et al. 2002), a secondary mark was utilized and both crews and fish wheel operators were made aware of the importance of examining fish for the presence of the secondary mark. Many thousands of fish have been examined for the presence of primary and secondary marks since the mark-recapture study was initiated in 1996 (Underwood et al. in press). In particular, fish captured in the Canadian fish wheels near the international border are tagged in an independent mark-recapture study, and large-scale tag loss would almost certainly have been noticed by the Canadian tagging crew. No incidence of tag loss has been conclusively documented from fish captured in the main-stem Yukon River, though one instance was reported during an interview of a fisher from Beaver, Alaska (Underwood et al. 2002). If tag loss was occurring at the magnitude necessary to explain the observed declines in mark rates (Figure 3), it is difficult to imagine that documentation of tag loss would be essentially absent. Even so, we recommend that the apparent lack of tag loss be conclusively documented, perhaps by taking photographs of randomly selected fish at upriver locations.

One might hypothesize that the decline in mark rates is attributable to a violation of the mark-recapture assumption that marked and unmarked fish mix completely before the recapture event (Seber 1982). It is possible that fish within the confines of the mark-recapture study are segregated such that the different components of the migrating population are tagged at different rates. The observed decline in mark rates would then be caused by the subsequent mixing of the segregated 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, 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., in press; Table 1; Figure 3). These samples have been obtained using a variety of gear types and in numerous locations, including all the known primary spawning grounds (Underwood et al., in press). 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 substantial body of evidence justifies a high level of confidence that the mixing assumption has been met, though it isn't conclusive. For example, the apparent mixing between the marking site and the Rampart recapture site could be a behavioral response to being tagged.

The mixing assumption would be violated if stocks of fish 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, for the most part, the results of this study provide some assurance that this did not occur in 2001. If stocks were differentially segregated by bank, the proportion of fish tagged on a particular bank would differ between stocks. However, the proportions of tagged fish recaptured at the Rampart, Circle, and Canadian sites that were tagged at the right-bank fish wheel were nearly equivalent to the proportion of all tagged fish originating from the right bank (Figure 15). Conversely, the proportion of fish recaptured at the Beaver site that originated from the right bank was significantly greater, though no biological reason for this difference is apparent. No populations of fall chum salmon are known to spawn between the Rampart and Beaver sites, or for many miles upriver of the Beaver site, so the stock composition of the migrating population is thought to have been the same at both locations. For that reason, the consistency of the data from the other three locations, and the small sample size obtained at the Beaver site (Table 1), we suspect this significant test result is spurious. However, this or a similar test should continue to be conducted whenever adequate data from upriver locations are available.

Although it is difficult to test the validity of the mixing assumption directly, we recommend that two additional data collection efforts be undertaken. Mark rate data from the Chandalar and Sheenjek rivers, two of the largest fall chum salmon stocks, are only available from one year (Underwood et al. in press). 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 that there is a segregation of fish on and off shore within the mark-recapture study area. If such a segregation was related to the ultimate destination of the fish, one would expect some stocks to have a mark rate exceeding that observed at the Rampart recapture site. As previously discussed, all mark rates observed within tributaries or in the upper Yukon River main-stem have been substantially less than that observed at Rampart (e.g., Underwood et al. in press). The apparent mixing of marked within the mark-recapture study area and the similarity between abundance estimates and run reconstructions provide some assurance that the mixing assumption is met. In addition, the abundance estimates appear reasonably consistent with data sources available from locations in the lower river (e.g., Pfisterer 2002; Cleary and Hamazaki 2002). Despite the apparent consistency among the available data sources, we recommend that a study be undertaken 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 will have to be carefully evaluated prior to conducting such a study.

The third potential cause of the decline in the mark rates is the PTM hypothesis. Underwood et al. (2000a) suggested that mortality upriver of the Rampart recapture site is the most likely cause of the decline. Underwood et al. (2002, in press) found that recapture rates decreased as the number of times fish were captured in fish wheels increased, which suggests that factors potentially causing PTM may be cumulative (Wedemeyer et al. 1990). We are not aware of any other investigations of PTM in which fish wheels were used, but numerous studies have documented stress or mortality associated with capture or handling of salmon or related species; recent examples include Cleary (2003), Buchanan et al. (2002), Budy et al. (2002), and Clements et al. (2002).

The results of this study are consistent with the PTM hypothesis. While the results are not conclusive, they are suggestive. Fish held in a live-box tended to have a higher probability of recapture at the marking site (Table 3), travel more slowly to the Rampart recapture site (Table 6, Figures 6-12), and have a higher probability of recapture at that site (Tables 4-5, Figure 4). Conversely, fish held for longer periods of time had a reduced probability of recapture at the upriver recapture sites (Table 7, Figures 13-14). One possible interpretation of these results is that holding fish in a live-box impairs their ability to sustain their migration severely enough that a portion of them drop out of the migrating population before reaching their natal streams. This apparent effect is certainly not manifested in all fish, but such tendencies are clearly present in the data. However, mark rates of fish that are not held also decline upriver (Figure 15), suggesting that negative effects may not be limited to fish that are held in a live-box. Rather, it appears that the decline in mark rates may be caused by factors we have not measured, perhaps the capture event itself, and that holding fish increases the severity of the response.

As previously discussed, fish handling methods were changed midway through the season. While we do not believe the modifications were sufficient to warrant separate treatment of the data from the two time periods, holding times were undoubtedly measured more precisely after the change was made. The results of this study should be verified by another year of investigation using the methods implemented in the latter portion of the 2001 season.

The quantity of data collected in 2001 was insufficient to support the analyses originally planned, i.e., use of a single multiple-event model, resulting in separate analyses of fish recaptured at Rampart and at upriver locations. The number of fish captured at Beaver, in particular, was less than desired, and the number of tagged fish captured at more than one location upriver of the Rampart recapture site was less than anticipated. Changes to methods that would be expected to generally increase sample sizes should be considered for implementation in 2002. A partial list of such changes includes increasing the number of tags deployed, finding a more efficient site for the Beaver fish wheel, operating the upriver fish wheels for more hours per day, and releasing all fish captured in the upriver fish wheels to maximize recaptures in multiple locations. In addition, given the large decline in mark rates between the Rampart and Beaver recapture locations, we recommend investigating the availability of an efficient fish wheel site in the vicinity of Stevens Village, Alaska as a potential location for an additional fish wheel.

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Table 1. Number of tagged fish released at the marking site and catches at the upriver recapture sites, by day.

		Rampart		Beaver		Circle		Canadian Border	
Date	Tags Released	Marked Catch	Total Catch	Marked Catch	Total Catch	Marked Catch	Total Catch	Marked Catch	Total Catch
07/30	99								
07/31	33	1	11						
08/01	64	3	42						
08/02	81	2	36					0	2
08/03	159	0	26						
08/04	317	2	66					0	4
08/05		5	120					0	4
08/06	294	20	337					0	4
08/07	299	14	423					0	3
08/08	298	23	481					0	2
08/09	290	20	600					0	1
08/10	277	22	529					0	2
08/11	272	19	524					0	2
08/12		25	456	0	16				
08/13	292	16	497	0	18	0	1		
08/14	265	11	450	1	54	0	4	0	1
08/15	117	12	388	1	33	0	1	0	1
08/16	271	8	315	2	48	0	11	0	1
08/17	239	10	294			0	22	0	2
08/18	264	26	338					0	2
08/19		13	203	0	24			0	4
08/20	257	17	224	0	28	1	78	0	1
08/21	285	15	306	1	24	2	146	0	5
08/22	305	24	341	0	11			0	8
08/23	273	7	279	1	39	0	47	0	13
08/24	295	14	249			3	113	0	23
08/25	279	9	335			4	145	0	33
08/26		13	311	1	35			3	40
08/27	236	21	539	3	59	5	132	0	43
08/28	275	11	483	1	55	4	77	1	60
08/29	267	17	357	1	64	0	68	2	59
08/30	233	14	308	1	34	1	68	0	56
08/31	248	11	250			0	78	1	57
09/01	227	13	211					1	42
09/02		5	190	2	31			0	51
09/03	221	5	171	0	38			2	76
09/04	149	6	174	0	36	0	142	3	91
09/05	203	11	172	0	25	4	160	0	90
09/06	127	1	136	0	35	6	129	2	105
09/07	97	6	90			2	186	0	154
09/08	100	8	90			1	87	6	245
09/09		7	95	0	32			3	198
09/10	90	3	57	2	10	1	82	1	204
09/11	97	2	60	1	11	0	53	2	185
09/12	92	1	26	0	14	0	48	4	168
09/13	96	2	63	0	10	0	41	1	117
09/14	54	1	40			1	128	1	89
09/15	53	0	30			3	105	1	87
09/16		0	55	0	8			0	104
09/17		5	27	0	4			1	71
09/18		0	9	0	1	0	98	2	98
09/19				1	3	0	22	2	116
09/20				0	5	1	26	2	49
09/21						0	14	2	47
09/22						1	23	1	59
09/23				0	1			2	83
09/24				0	1	1	19	0	78
09/25				0	0	0	14	1	54
09/26				0	0	1	9	0	44
09/27						0	4	1	29
09/28						0	4	1	33
09/29						0	2	1	35
09/30								0	10
10/01								1	14
10/02								0	7
10/03								0	5
10/04								0	6
Total	8,490	501	11,814	19	807	42	2,387	51	3,277

Table 2. Number of fall chum salmon by capture history.

Number Of Fish	Number of Times Fish Were Captured at Each Location					
	Marking	Rampart	Beaver	Circle	Canadian	Total
7,399	1	0	0	0	0	1
445	1	1	0	0	0	2
10	1	2	0	0	0	3
2	1	1	1	0	0	3
1	1	1	0	1	0	3
1	1	1	0	0	1	3
15	1	0	1	0	0	2
41	1	0	0	1	0	2
46	1	0	0	0	1	2
2	1	0	0	0	2	3
449	2	0	0	0	0	2
35	2	1	0	0	0	3
1	2	2	0	0	0	4
1	2	0	1	0	0	3
1	2	0	0	0	1	3
22	3	0	0	0	0	3
5	3	1	0	0	0	4
1	4	0	0	0	0	4

Table 3. Parameter estimates and inferential statistics for the generalized linear model of the probability a tagged fish is recaptured at the marking site.

Parameter	Estimate	Standard Error	Chi-square Test Statistic	Degrees Of Freedom	Significance
Intercept - Stratum 1	-2.6310	1.4122	3.5	1	0.0625
Intercept - Stratum 2	-1.2649	1.3958	0.8	1	0.3648
Intercept - Stratum 3	-1.5606	1.3887	1.3	1	0.2611
Intercept - Stratum 4	-1.4969	1.3933	1.2	1	0.2827
Intercept - Stratum 5	-4.0527	1.4031	8.3	1	0.0039
Intercept - Stratum 6	-4.0320	1.4078	8.2	1	0.0042
Intercept - Stratum 7	-3.9626	1.4193	7.8	1	0.0052
Sex (Female)	-6.0547	1.9164	10.0	1	0.0160
Length	-0.0303	0.0232	1.7	1	0.1916
Holding Time	1.8628	0.1473	159.9	1	< 0.0001
Crowding	-0.0528	0.0057	84.4	1	< 0.0001
Sex - Length	0.1051	0.0326	10.4	1	0.0013
Holding Time - Crowding	0.0202	0.0023	75.1	1	< 0.0001

Table 4. Parameter estimates and inferential statistics for the generalized linear model of the probability a tagged fish is recaptured at the Rampart recapture fish wheel.

Parameter	Estimate	Standard Error	Chi-square Test Statistic	Degrees Of Freedom	Significance
Intercept - Stratum 1	-2.8014	0.1636	293.2	1	< 0.0001
Intercept - Stratum 2	-2.6469	0.0956	766.9	1	< 0.0001
Intercept - Stratum 3	-2.6730	0.1054	643.6	1	< 0.0001
Intercept - Stratum 4	-2.9536	0.1119	696.4	1	< 0.0001
Intercept - Stratum 5	-3.5933	0.1669	463.3	1	< 0.0001
Intercept - Stratum 6	-3.6333	0.2054	312.9	1	< 0.0001
Intercept - Stratum 7	-4.6149	0.3751	151.3	1	< 0.0001
Holding Time	0.3634	0.0751	23.4	1	< 0.0001

Table 5. Summary statistics for the proportion of marked fish that are recaptured at the Rampart recapture site, jointly classified by marking stratum and binned categories of holding time in a live-box.

Holding Time	Statistic	Stratum 1	Stratum 2	Stratum 3	Stratum 4	Stratum 5	Stratum 6	Stratum 7
	Sample Size	163	959	516	449	255	106	29
0	Sample Proportion	0.0368	0.0688	0.0698	0.0757	0.0078	0.0189	0.0345
	Standard Error	0.0148	0.0082	0.0112	0.0125	0.0055	0.0133	0.0345
	Sample Size	86	748	776	905	420	23	50
0.5	Sample Proportion	0.0465	0.0695	0.0760	0.0453	0.0381	0.0435	0.0000
	Standard Error	0.0228	0.0093	0.0095	0.0069	0.0094	0.0435	0.0000
	Sample Size	447	14	152	327	564	633	371
1.5	Sample Proportion	0.1029	0.0714	0.0724	0.0734	0.0550	0.0490	0.0108
	Standard Error	0.0144	0.0714	0.0211	0.0144	0.0096	0.0086	0.0054
	Sample Size	42	1	3	10	222	101	21
2.5	Sample Proportion	0.1667	0.0000	0.0000	0.2000	0.0495	0.0297	0.0476
	Standard Error	0.0582	*	0.0000	0.1333	0.0146	0.0170	0.0476
	Sample Size	11	1	0	2	18	28	11
3.5	Sample Proportion	0.1818	0.0000	*	0.0000	0.0556	0.0714	0.1818
	Standard Error	0.1220	*	*	0.0000	0.0556	0.0496	0.1220
	Sample Size	1	0	0	0	5	4	0
4.5	Sample Proportion	0.0000	*	*	*	0.2000	0.2500	*
	Standard Error	*	*	*	*	0.2000	0.2500	*
	Sample Size	0	0	0	0	1	2	0
5.5	Sample Proportion	*	*	*	*	0.0000	0.0000	*
	Standard Error	*	*	*	*	*	0.0000	*

Table 6. Parameter estimates and inferential statistics for the generalized linear model of the travel time between the marking site and the Rampart recapture fish wheel.

Parameter	Estimate	Standard Error	Chi-square Test Statistic	Degrees Of Freedom	Significance
Intercept - Stratum 1	-0.1441	1.1533	0.0	1	0.9006
Intercept - Stratum 2	-1.0039	1.0851	0.9	1	0.3549
Intercept - Stratum 3	-0.6047	1.0899	0.3	1	0.5790
Intercept - Stratum 4	-1.0621	1.0810	1.0	1	0.3259
Intercept - Stratum 5	-1.7707	1.0398	2.9	1	0.0886
Intercept - Stratum 6	-1.6473	1.0422	2.5	1	0.1140
Intercept - Stratum 7	-2.0728	1.1120	3.5	1	0.0623
Sex (Female)	0.6729	0.1175	32.8	1	< 0.0001
Length	0.0530	0.0181	8.6	1	0.0035
Holding Time	0.2324	0.0957	5.9	1	0.0151

Table 7. Parameter estimates and inferential statistics for the generalized linear model of the probability a tagged fish is recaptured in the Beaver, Circle, or Canadian fish wheels.

Parameter	Estimate	Standard Error	Chi-square Test Statistic	Degrees Of Freedom	Significance
Intercept	-4.0298	0.1198	1130.7	1	< 0.0001
Holding Time	-0.5197	0.1541	11.4	1	0.0007

Table 8. Summary statistics of travel time, in days, between the marking site and upriver recapture locations.

Recapture Location	Distance (km)	Number Of Fish	Mean	Standard Deviation	Minimum	Maximum	Migration Rate (km/d)
Rampart	52	500	2.9	2.0	1	18	18.2
Beaver	323	18	8.3	1.4	7	12	38.8
Circle	531	42	17.9	3.8	13	30	29.7
Canadian	793	50	23.1	3.2	18	32	34.4

Table 9. Parameter estimates and inferential statistics for generalized linear models of the proportion of catches in the recapture fish wheels as a function of the distance from the marking site, by fish category.

Fish Category	Parameter	Estimate	Standard Error	Chi-square Test Statistic	Degrees Of Freedom	Significance
Fish Not Held	Intercept	-4.3035	0.0907	2253.7	1	< 0.0001
	Distance	-14.4636	3.2462	19.9	1	< 0.0001
Fish Held	Intercept	-3.4102	0.0594	3300.6	1	< 0.0001
	Distance	-15.9274	2.1871	53.0	1	< 0.0001
Fish Held > 0.5 hr	Intercept	-3.8157	0.0730	2730.8	1	< 0.0001
	Distance	-19.1417	2.9352	42.5	1	< 0.0001

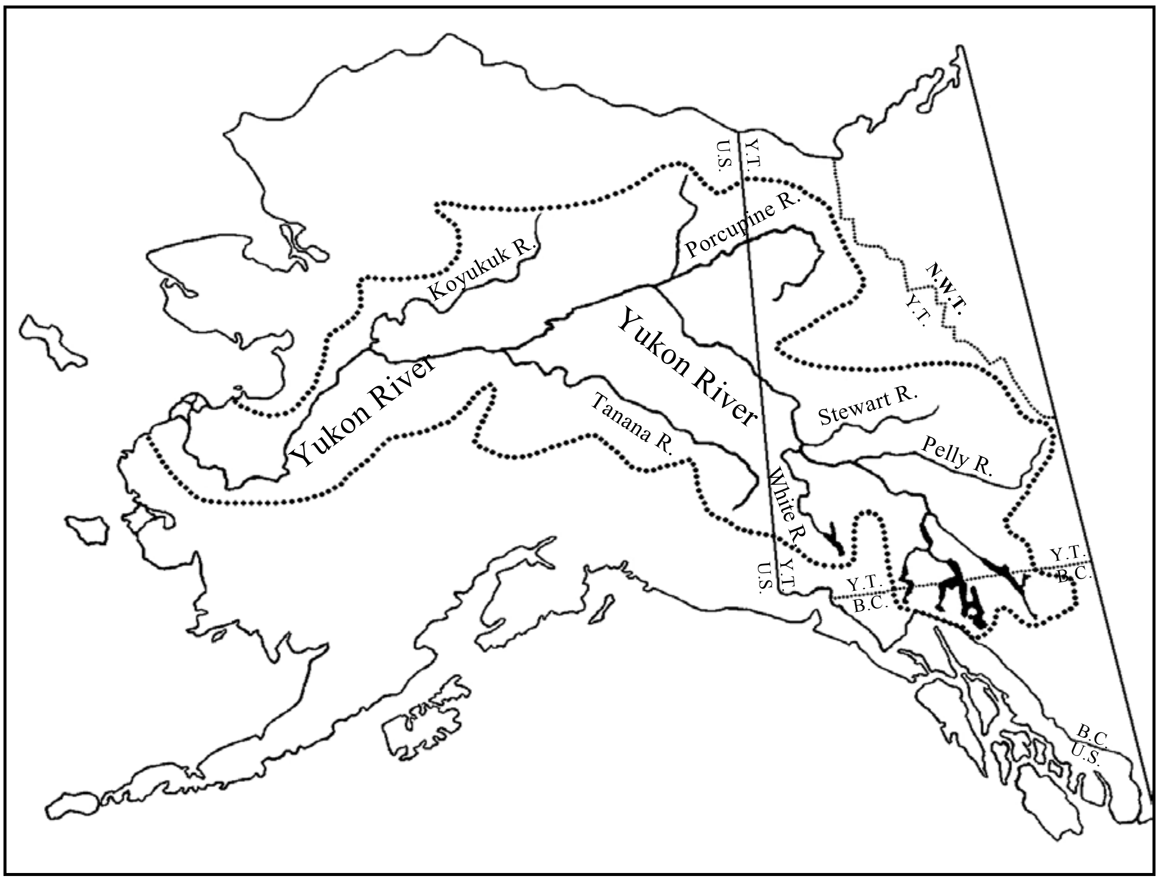


Figure 1. Map of the Yukon River drainage in Canada and Alaska.

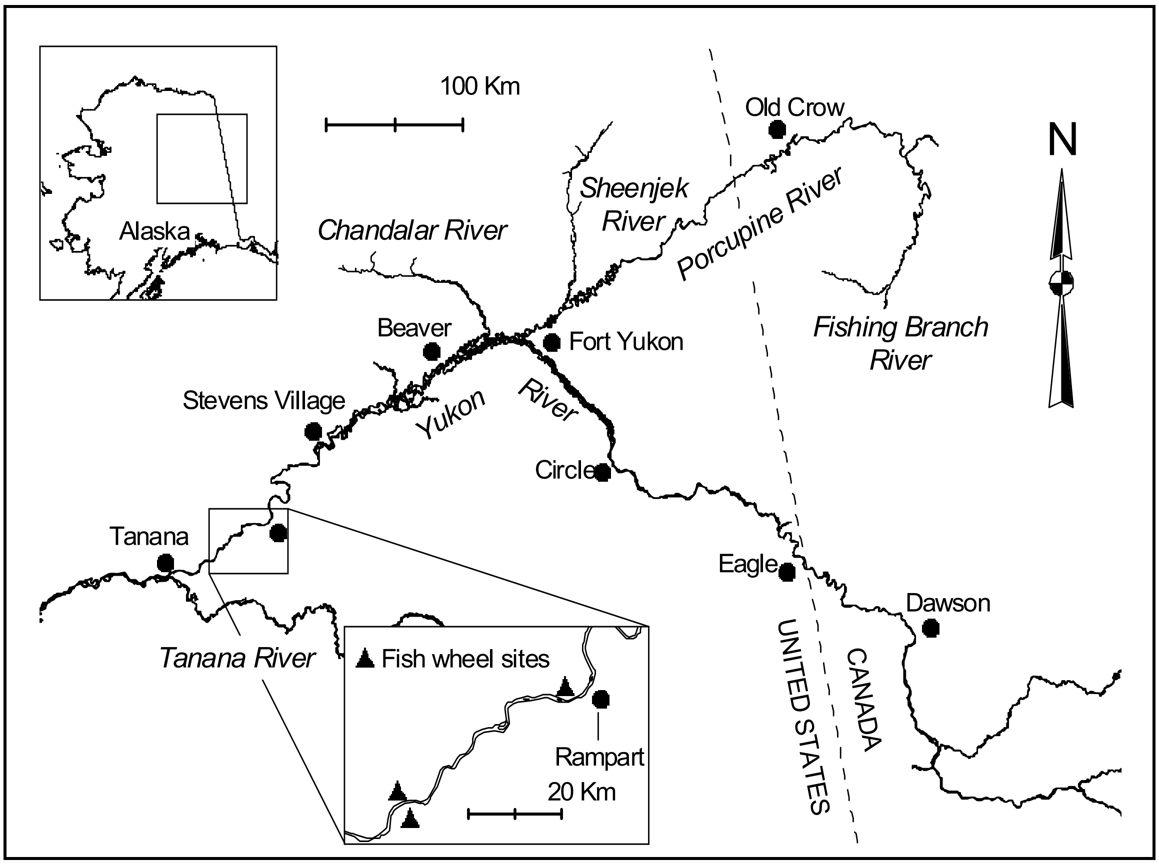


Figure 2. Map of the mark-recapture study site within the Yukon River drainage.

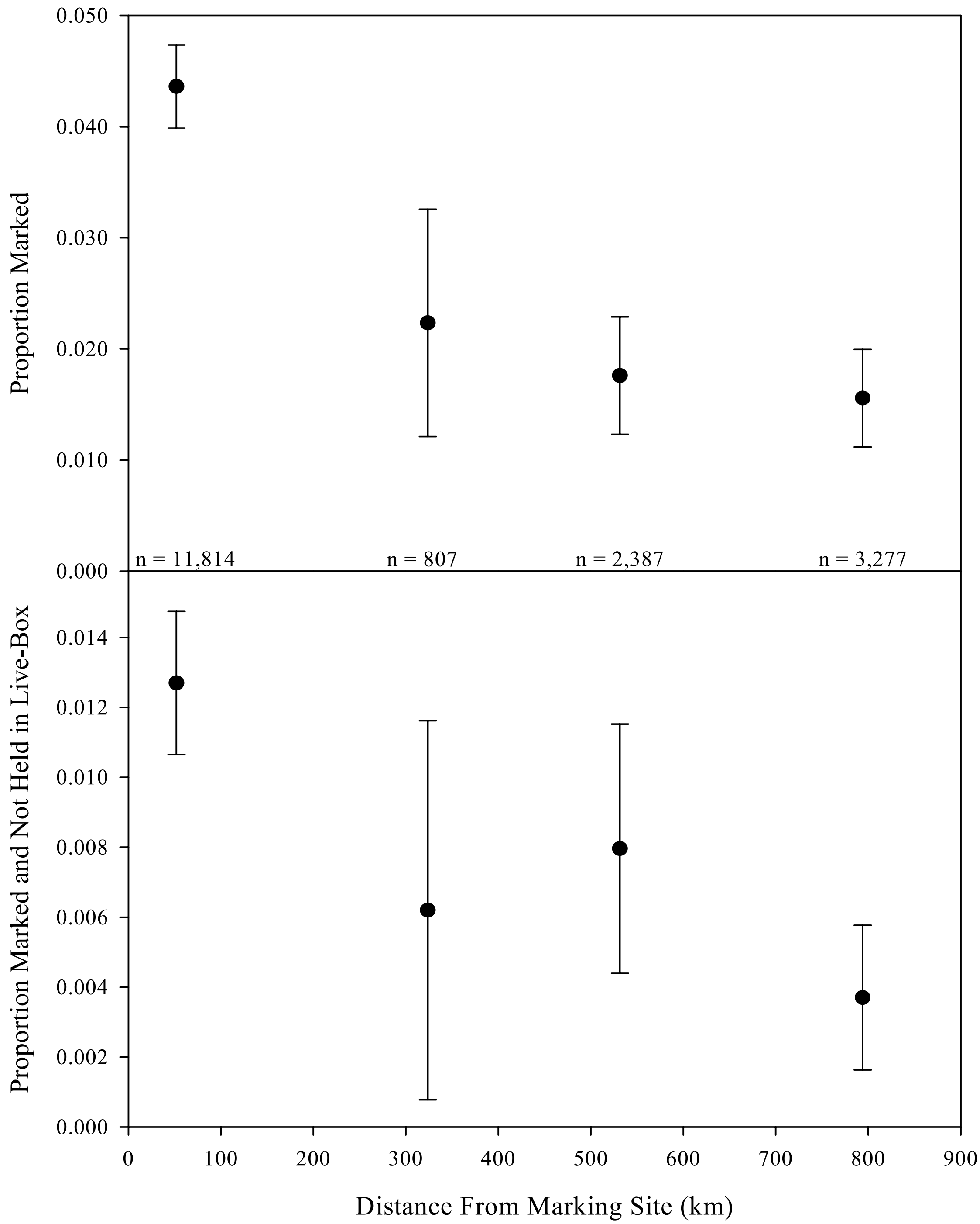


Figure 3. Mark rates observed in the recapture fish wheel catches (top) and the proportions of the catches consisting of marked fish that had not been held in a live-box (bottom), with 95% confidence intervals, versus distance from the marking site.

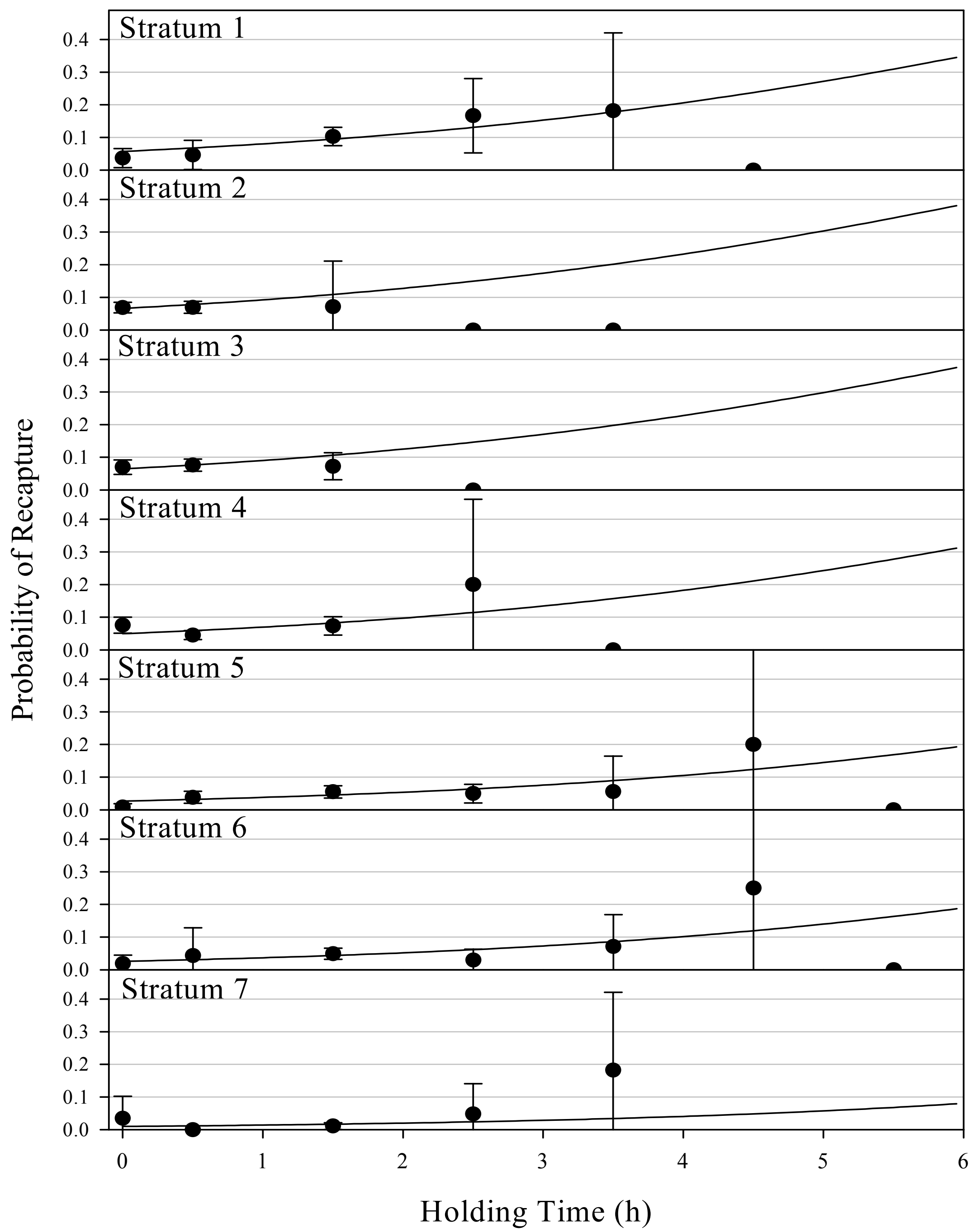


Figure 4. Model of the probability a tagged fish is captured in the Rampart recapture fish wheel, contrasted with the observed recapture proportions and 95% confidence intervals, as a function of binned holding time categories.

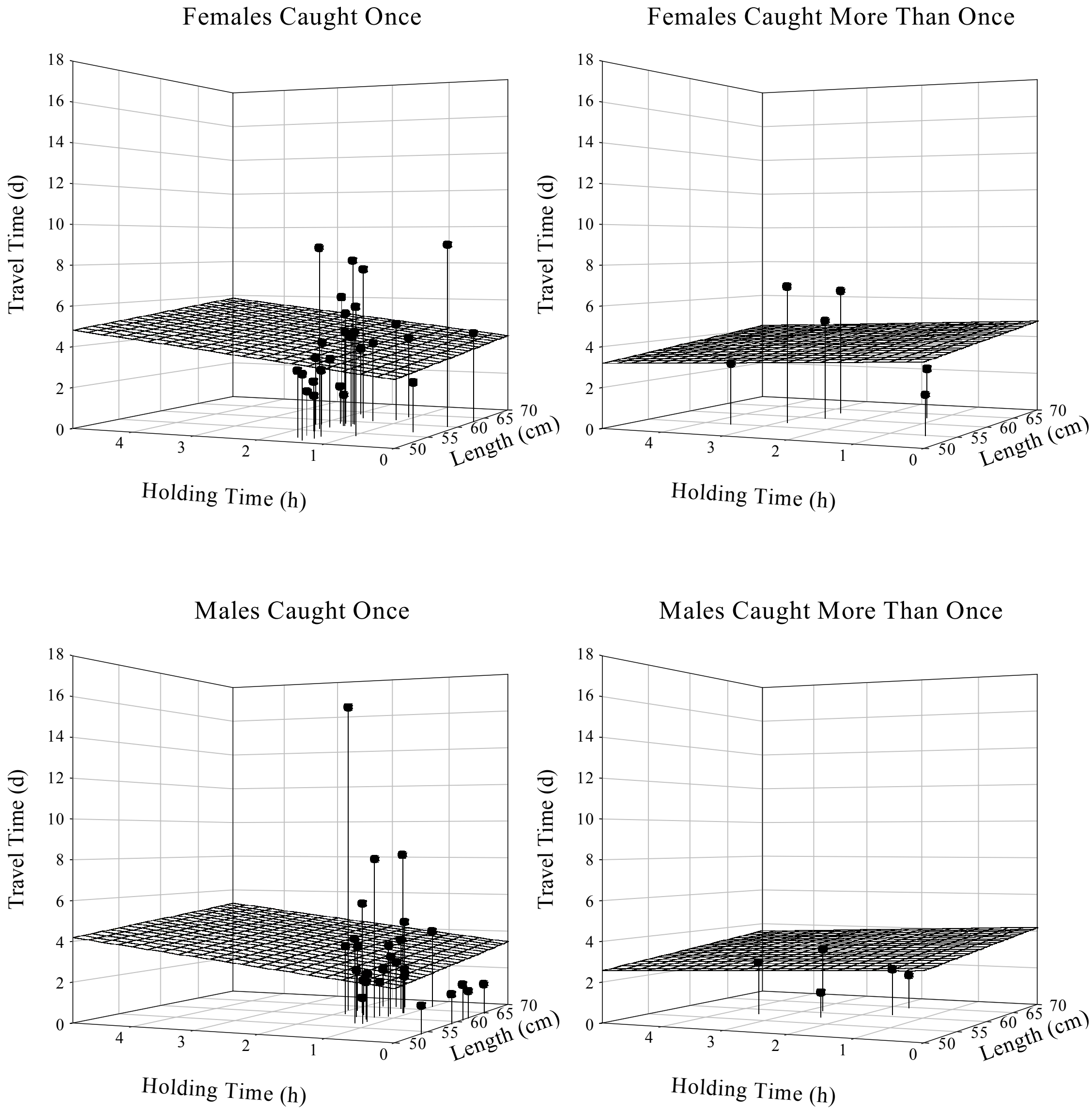


Figure 5. Plot of an intermediate model (plane), with a statistically significant interaction, of travel time between the marking site and the Rampart recapture site for fish released during marking stratum 1, with observed data (circle).

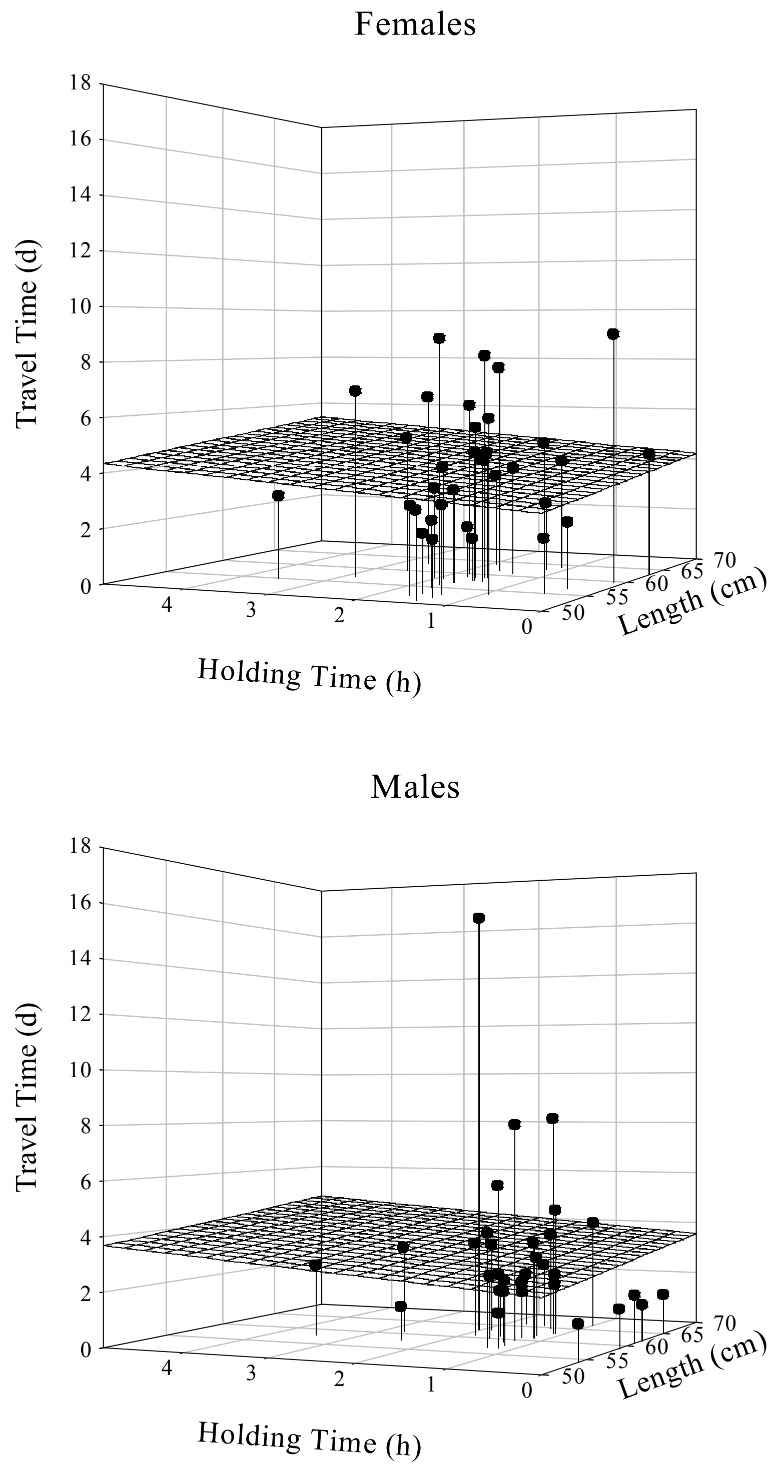


Figure 6. Estimated model (plane) and observed data (circles) of travel time between the marking site and the Rampart recapture site for fish released in marking stratum 1.

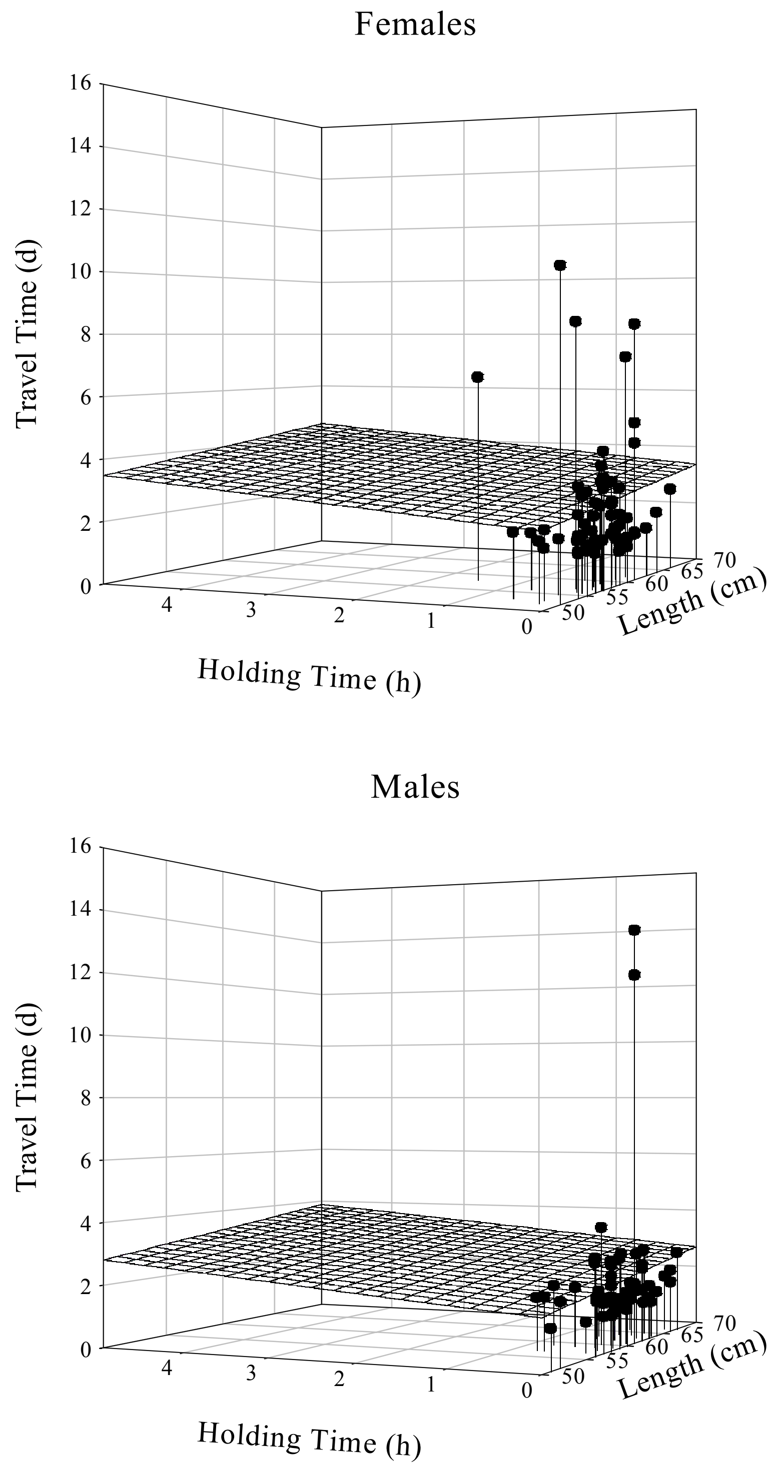
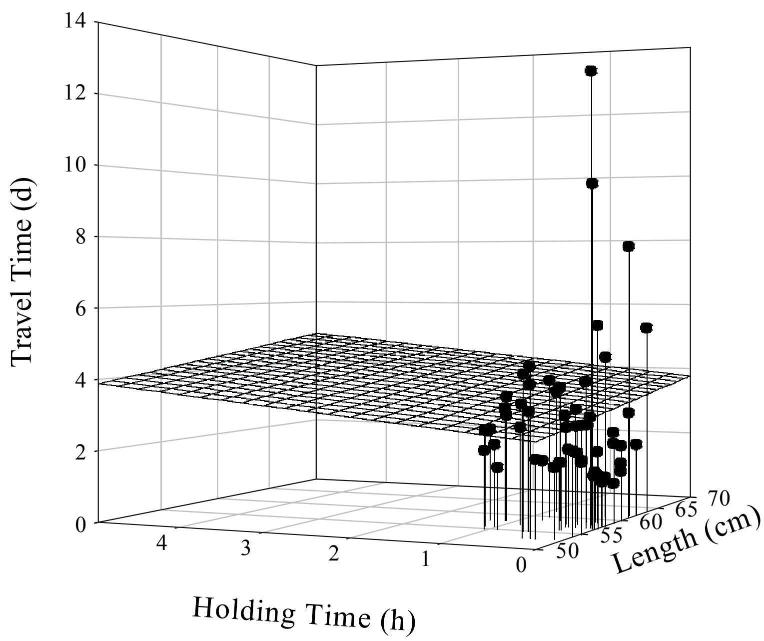


Figure 7. Estimated model (plane) and observed data (circles) of travel time between the marking site and the Rampart recapture site for fish released in marking stratum 2.

Females



Males

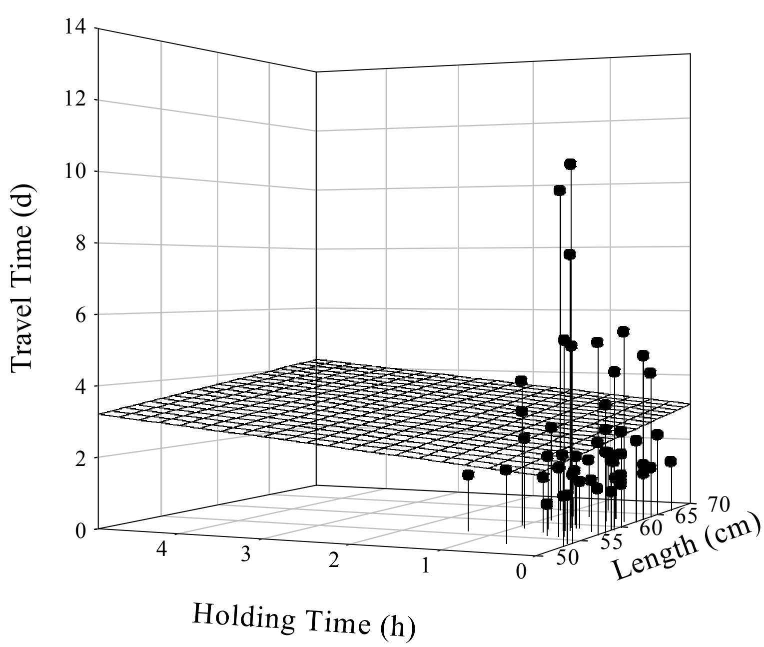


Figure 8. Estimated model (plane) and observed data (circles) of travel time between the marking site and the Rampart recapture site for fish released in marking stratum 3.

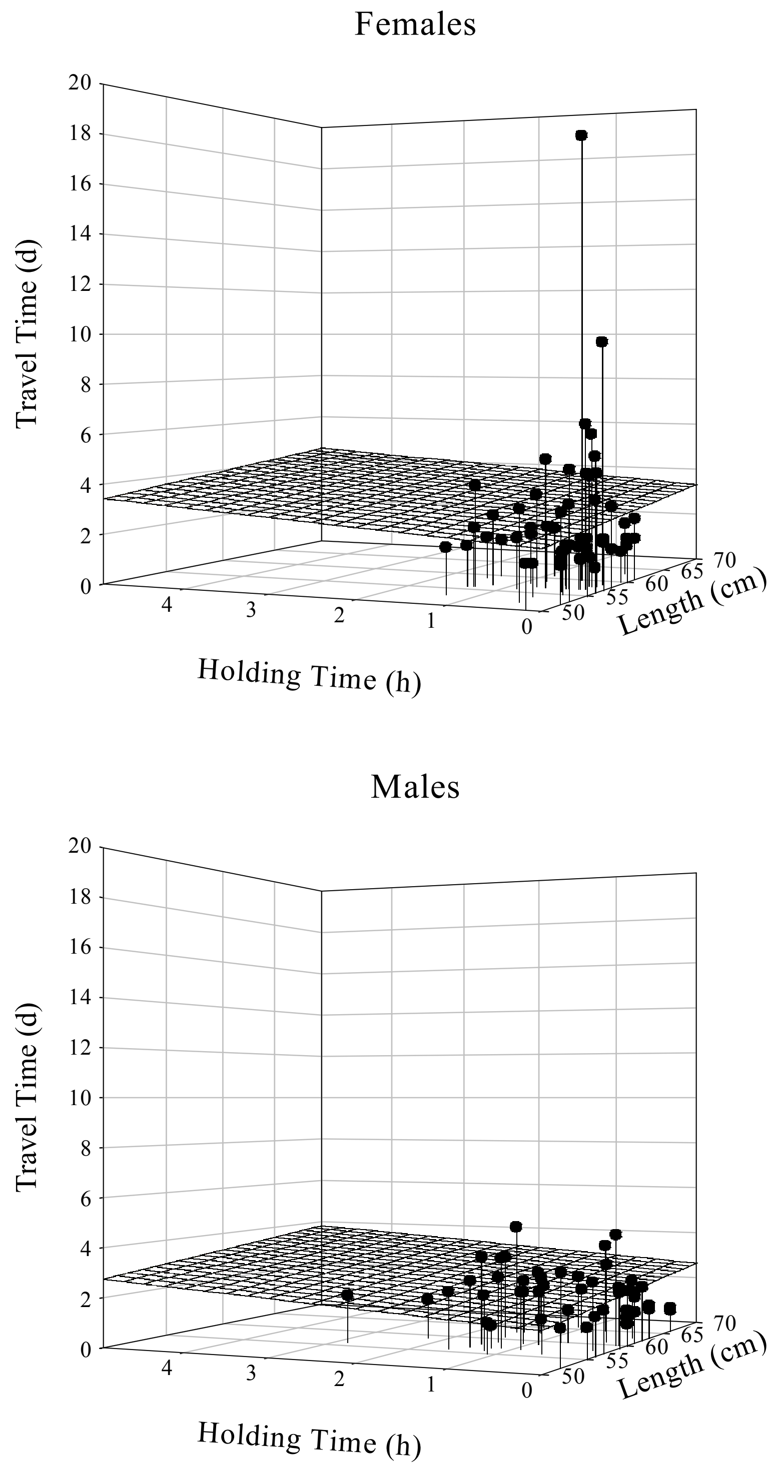


Figure 9. Estimated model (plane) and observed data (circles) of travel time between the marking site and the Rampart recapture site for fish released in marking stratum 4.

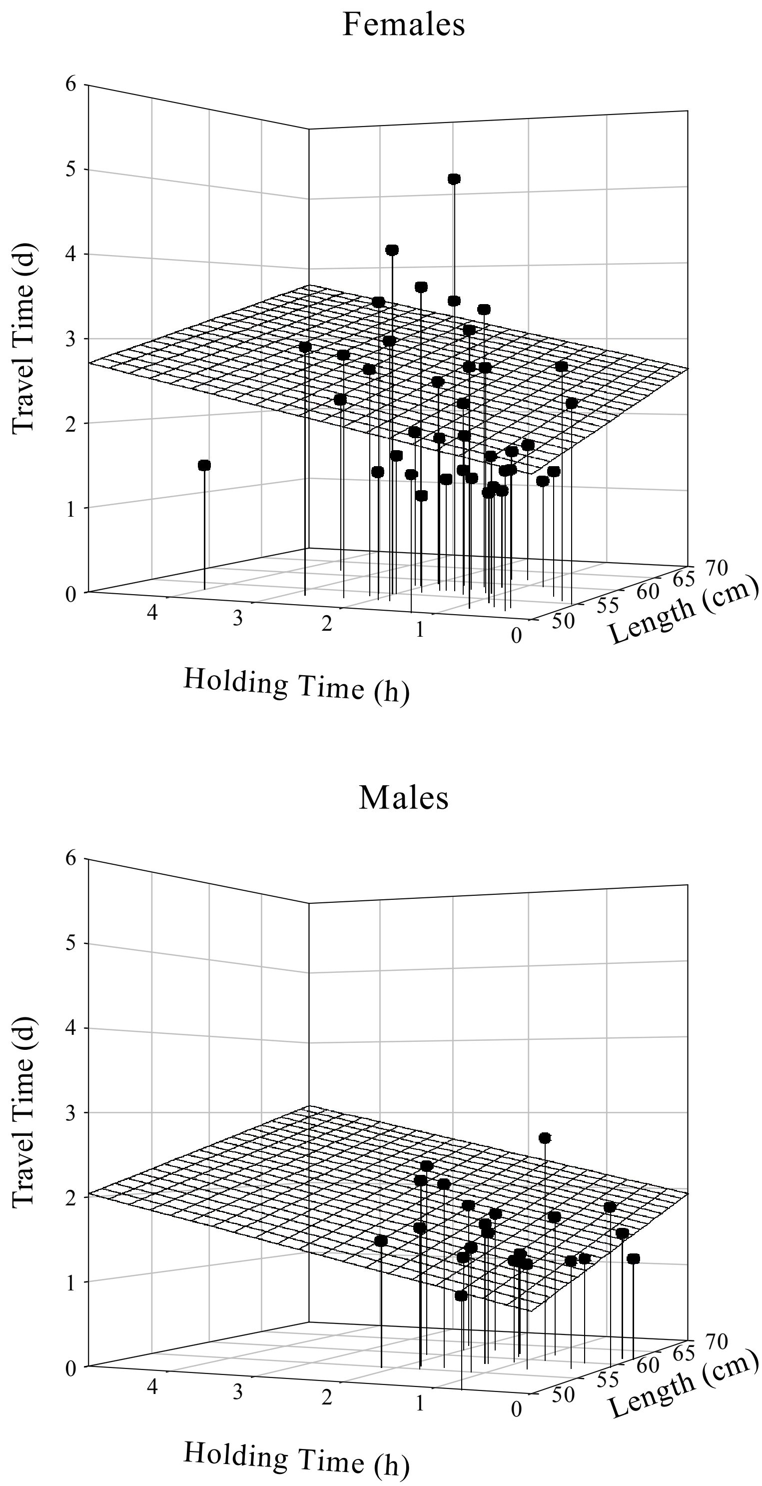


Figure 10. Estimated model (plane) and observed data (circles) of travel time between the marking site and the Rampart recapture site for fish released in marking stratum 5.

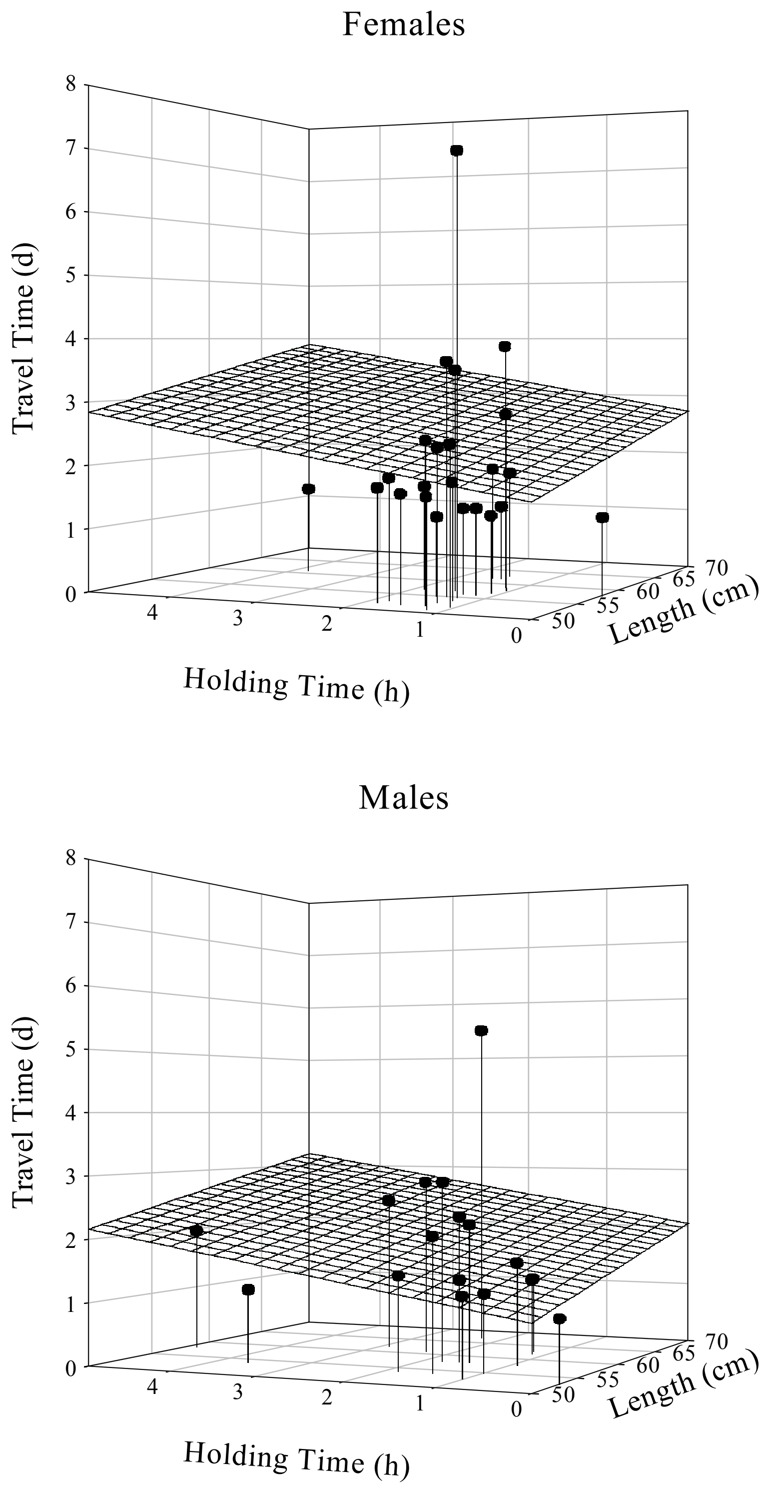
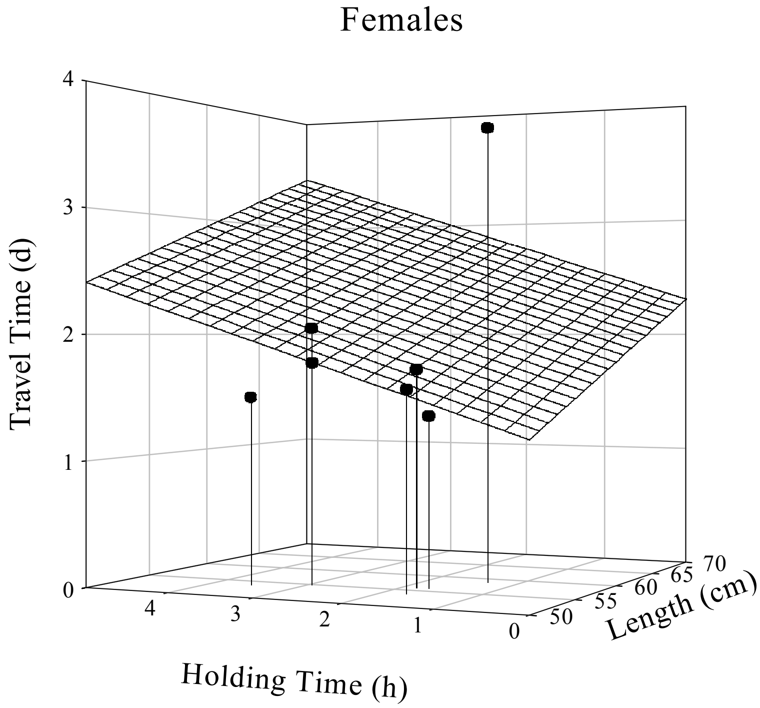


Figure 11. Estimated model (plane) and observed data (circles) of travel time between the marking site and the Rampart recapture site for fish released in marking stratum 6.



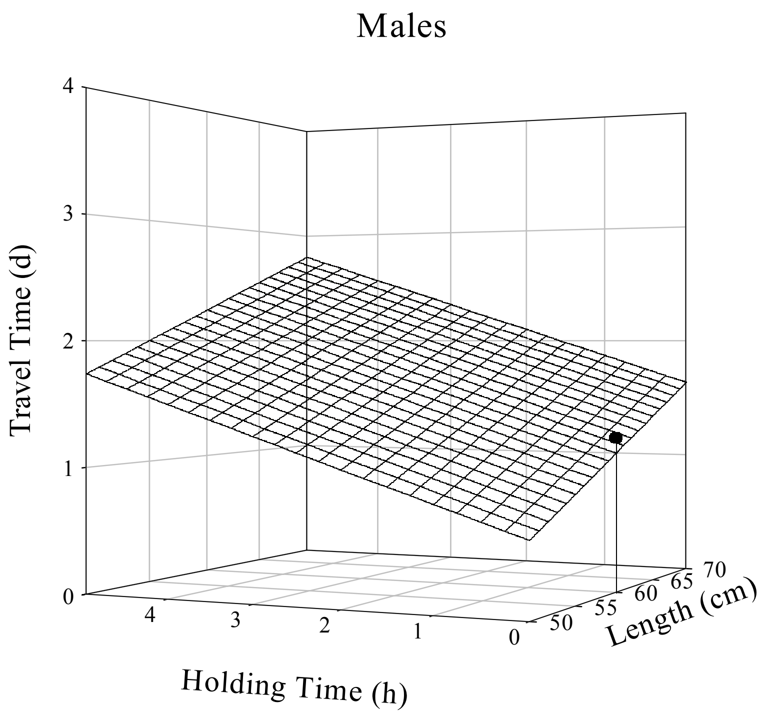


Figure 12. Estimated model (plane) and the observed data (circles) of travel time between the marking site and the Rampart recapture site for fish released in marking stratum 7.

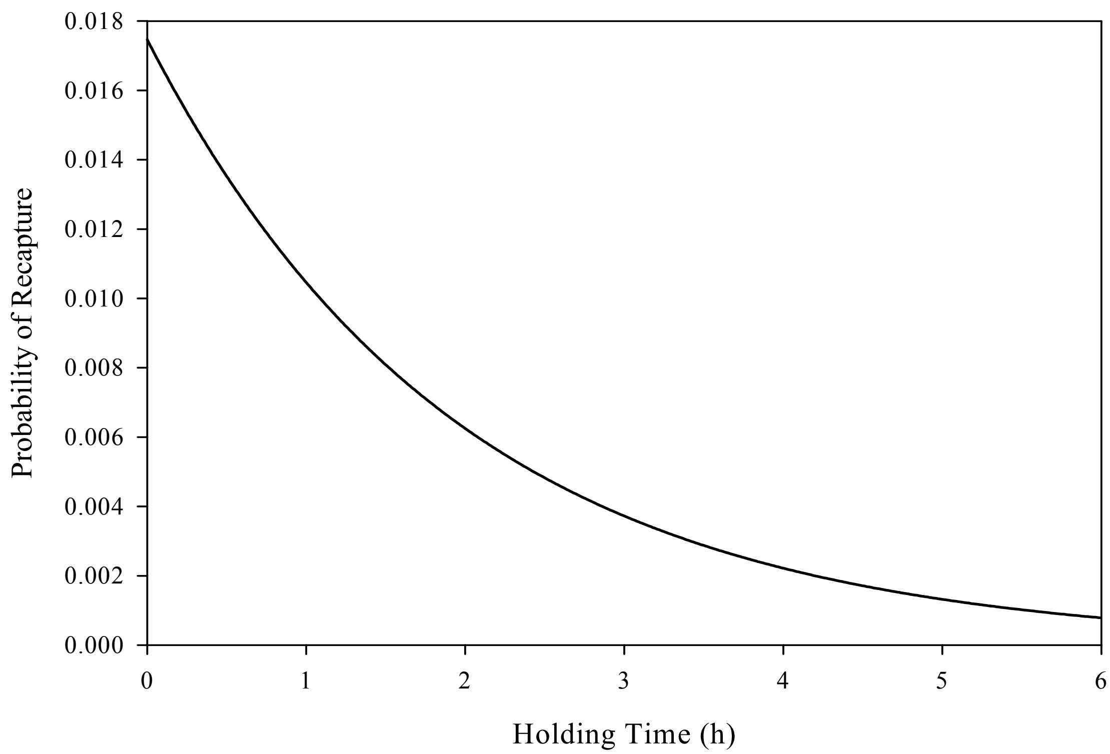


Figure 13. Estimated model of the probability a tagged fish is recaptured in the Beaver, Circle, or Canadian recapture fish wheels.

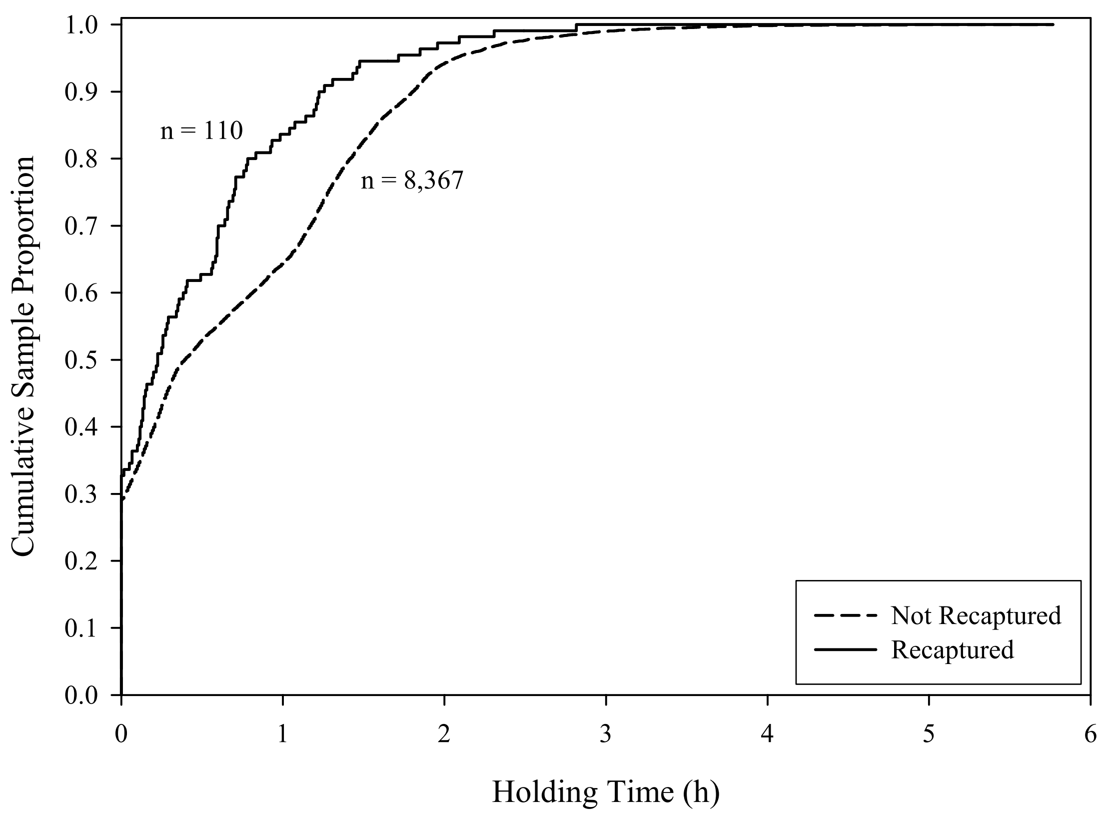


Figure 14. Observed cumulative distributions of holding time for fish that were and were not recaptured in the Beaver, Circle, or Canadian recapture fish wheels.

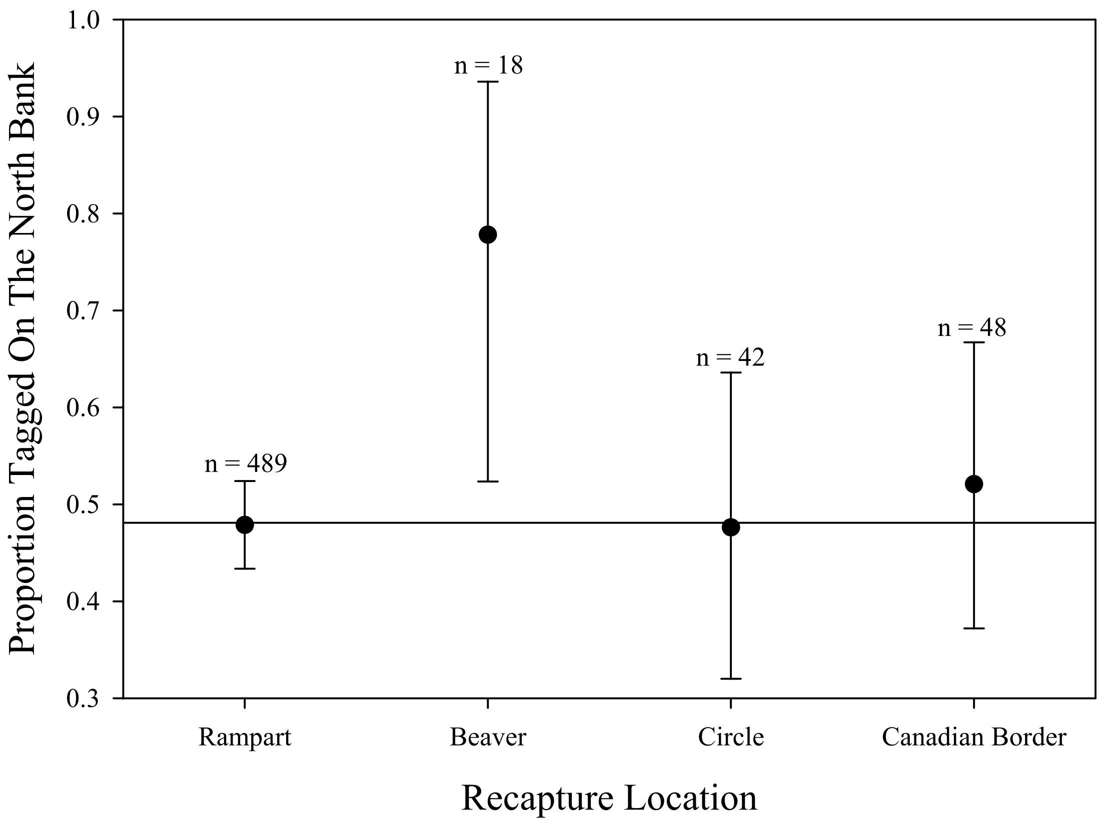


Figure 15. The proportion of recaptured fish that were initially tagged at the right-bank marking fish wheel, with exact 95% confidence limits, by recapture location.

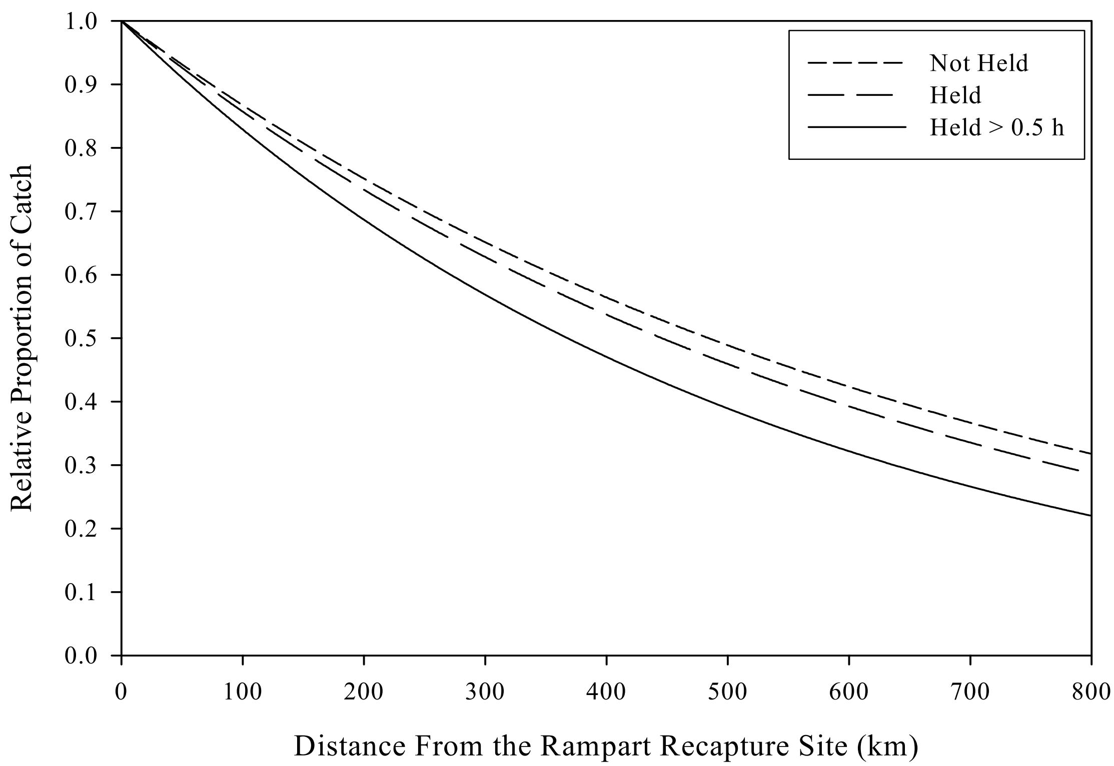


Figure 16. Models of the relative proportion of a catch consisting of fish that had not been held, had been held for any length of time, and had been held for at least 0.5 h as a function of distance from the Rampart recapture site.