

Survival and Migration Behavior of Juvenile Coho Salmon in the Klamath River
Relative to Discharge at Iron Gate Dam, 2006

Final Report Prepared for:

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Submitted: 31 December 2007

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ACKNOWLEDGEMENTS

We thank Ron Costello, Rich Piaskowski, and others at the U. S. Bureau of Reclamation for their cooperation and assistance on this study. We would also like to thank Kim Rushton and his staff at the Iron Gate Hatchery (operated by California Department of Fish and Game) and Bill Chesney (also of California Department of Fish and Game) and his crew operating the Shasta River rotary screw trap, for capturing the wild juvenile coho salmon used in this study. We thank our collaborators with the Karuk and Yurok Tribes of California for their assistance. Lastly, we thank our colleagues at the USGS Columbia River Research Laboratory and USFWS Arcata Fish and Wildlife Office. Funding for this project was provided by the U. S. Bureau of Reclamation, Mid-Pacific Region, Klamath Basin Area Office, Klamath Falls, Oregon, Contracts 06AA204092 and 07AA200181. Reference to trade, firm, or corporation names does not imply endorsement by the U. S. Department of Interior or the U. S. Geological Survey.

SUGGESTED CITATION FORMAT

Beeman, J. W., G. M. Stutzer, S. D. Juhnke, N. J. Hetrick. 2007. Survival and migration behavior of juvenile coho salmon in the Klamath River relative to discharge at Iron Gate Dam, 2006. Final report prepared by U. S. Geological Survey, Cook, Washington and U. S. Fish and Wildlife Service, Arcata, California for the U. S. Bureau of Reclamation, Mid-Pacific Region, Klamath Basin Area Office, 06AA204092 and 07AA200181, Klamath Falls, Oregon.

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EXECUTIVE SUMMARY

This report describes a study of survival and migration behavior of juvenile coho salmon in the Klamath River relative to discharge at Iron Gate Dam in 2006. This was the second year of a multi-year study with the goal of determining the effects of discharge at Iron Gate Dam on survival of juvenile coho salmon downstream. The study was a collaborative effort among U.S. Geological Survey (USGS), U.S. Fish and Wildlife Service (USFWS), and the Yurok and Karuk Tribal Fisheries Departments. The goals of the study included: 1) estimating the survival of wild and hatchery juvenile coho salmon in the Klamath River downstream from Iron Gate Dam, 2) determining the effects of discharge and other covariates on their survival and migration, and 3) determining if fish from Iron Gate Hatchery could be used as surrogates for the limited source of wild fish. The major findings of the study in 2006 include:

River discharges during the 2006 study period (4 April through 21 July 2006) were among the greatest on record. Average daily discharge at Iron Gate Dam was 3,956 cubic feet per second (cfs) and ranged from 997 to 10,300 cfs. Discharge at Iron Gate Dam was positively correlated with discharges of tributaries downstream due to the above average water year and frequent occurrence of spill at Iron Gate Dam. Average daily discharge near the estuary was 25,789 cfs and ranged from 4,740 to 50,600 cfs.

This study was based on hatchery fish taken directly from a tank at Iron Gate Hatchery and wild fish captured in a rotary trap on the Shasta River. Releases of both groups began on 4 April when the catch of wild fish in California Department of Fish and Game's Shasta River rotary trap increased, but trap catches varied throughout the study period, resulting in differences in release dates of hatchery and wild fish. A total of 211 hatchery fish were released from 4 April through 26 May. Wild and hatchery fish released on a regular schedule between 25 April and 16 May 2006 were used in comparisons of the survival and migration of hatchery ($N = 120$) and wild ($N = 162$) fish. Additional analyses were performed using hatchery fish from all dates.

The data and models did not support clear differences between survivals of hatchery and wild fish released on common dates, so estimates of reach survivals were made after pooling these data. Estimates of survival were lowest in the Iron Gate Dam to Scott River reach (0.813) and greatest in the Salmon River to Trinity River reach (1.000). The overall survival from river kilometer 309 (Iron Gate Hatchery) to river kilometer 33 was 0.653 (95% CI 0.578 to 0.729). Estimates of survival based on all hatchery fish releases were similar to those from release dates common to hatchery and wild fish and are similar to those in other river systems over similar distances.

The migrations of hatchery and wild fish were different in the uppermost sections of the study area and were similar thereafter. A lag between release and migration, primarily upstream from the Scott River (river kilometer 234), was present in hatchery fish to a greater extent than in wild fish, resulting in differences in migration rates. Fish from both origins spent more time between release and the Scott River than in individual reaches downstream, and this was the only reach in which travel times of fish increased as discharge decreased. The travel times of hatchery and wild fish between sites were statistically similar downstream from Indian Creek (river kilometer 178).

There were differences and similarities in the analyses of the effects of covariates on survivals of hatchery and wild fish. The models of covariate effects based on hatchery and wild fish released on common dates indicated effects on wild fish survival that were not supported in data from hatchery fish. However, when the entire suite of hatchery fish releases were used the results of the analyses were similar to those based on wild fish. In both instances the effects of temperature and release date were primarily in the first reach, the reach fish of both origins spent most of their time within. The signs of the effects of these covariates differed among the fish origins (negative for wild and positive for hatchery fish), presumably due to differences in their migrations in the first reach. The effects of dam discharge on survivals of hatchery and wild fish were generally similar (positive relation), and the effects on hatchery, and to a lesser extent wild, fish were largely downstream from the Scott River. This is likely due to the prolonged

residence of the naïve hatchery fish, and to a lesser extent, migrant wild fish between release and the Scott River. Inasmuch as the differences between hatchery and wild fish we observed were likely those of migrants vs. non-migrants, the use of hatchery fish captured as they are migrating downstream, rather than those directly from hatchery tanks (i.e., naïve), may improve similarities between hatchery and wild fish in future studies.

The data and models used in 2006 do not support the use of naïve hatchery fish as surrogates for migrant wild fish in determining the effects of discharge on survival upstream from the Scott River. This conclusion is based on the different effects of covariates in this reach that were likely attributable to the differences in hatchery and wild migration behaviors in this reach.

The results of this second year of research provide insight to the migration and survival of hatchery and wild juvenile coho salmon in the Klamath River, but the results are from a single unusual water year. The results may be different during other water year types. The current information supports a positive relation between discharge at Iron Gate Dam and survival of juvenile coho salmon downstream, but additional data should be used to refine this relation. Discharge at the dam was correlated with discharges of Klamath River tributaries during this above average water year. The data and models from the 2006 study provide the first estimates of survival of these fish in the Klamath River and can be used with data from years with other water year types to examine the effects of discharge on survival. This will only be possible over a period of years in which the correlations between discharge and other factors, such as water temperature and date, are diminished. An experimental approach in which discharges are varied at Iron Gate Dam is the most direct method to determine if survivals are affected by discharge, but this may not be feasible given the limited storage capacity of the project.

INTRODUCTION

Coho salmon (*Oncorhynchus kisutch*) is a species of Pacific salmon inhabiting most major river systems of the Pacific Rim from central California to northern Japan (Laufle et al. 1986). Several investigations have documented extinction of local populations of coho salmon in Washington, Oregon, Idaho, and California (Nehlsen et al. 1991; Frissel 1993; Brown et al. 1994). A status review of coho salmon populations from Washington, Oregon, and California (Weitkamp et al. 1995) prompted the National Marine Fisheries Service (NMFS) to list coho salmon populations within the Southern Oregon Northern California (SONC) Evolutionary Significant Unit (ESU) as threatened under the Endangered Species Act (ESA) on 6 May 1997.

The U.S. Bureau of Reclamation operates the Klamath Project to provide water to approximately 240,000 acres of cropland in three counties in southern Oregon and northern California. The Klamath Project relies primarily on water stored in Upper Klamath Lake near Klamath Falls, Oregon, but also includes water from Clear Lake Reservoir, Gerber Reservoir, and the Lost River. Several dams present on the Klamath River between Upper Klamath Lake and the Pacific Ocean are used to regulate water releases to the Klamath River and generate electricity, though their reservoirs provide little or no storage capacity (NRC 2001). PacifiCorp currently owns and operates Link River, Keno, J. C. Boyle, Copco #1, Copco #2, and Iron Gate dams subject to Klamath Project rights. Iron Gate Dam (IGD) located at river kilometer 310 is the lowermost dam on the Klamath River.

The Klamath River and its watershed encompass more than 40,403 km² in northern California and southern Oregon. Principal tributaries to the Klamath River include the Trinity, Salmon, Scott, and Shasta rivers. The majority of the middle and lower watershed is mountainous with intermittent small valleys. The upper watershed, which contains upper and lower Klamath, Tule, and Clear lakes, consists of several large valleys and closed basins bordered by mountains. Dense coniferous forests along the coast, where annual precipitation values are some of the highest in the contiguous United States,

give way to more Mediterranean conditions and vegetation in the middle and upper watershed.

Maintenance and restoration of anadromous fish populations requires sufficient stream flows to provide adequate habitat for spawning and rearing throughout the freshwater phase of their life cycle, as well as during the downstream migration of juvenile fish to the ocean (Cada et al. 1997). Coho salmon evolved in free-flowing rivers in which downstream migration of juveniles was often associated with high spring stream flows. In the Klamath River system, flows are now impeded by water storage reservoirs and reduced by water diversions, resulting in decreased water velocities. Lower water velocities in the spring may slow the downstream migration of juveniles and decrease juvenile salmon survival by increasing exposure to predation and disease (Cada et al. 1997; Clements and Schreck 2003). Additionally, delayed migration may impair the osmoregulatory ability of juvenile salmon entering the marine environment (Berggren and Filardo 1993).

In May 2001 the National Marine Fisheries Service (now NOAA Fisheries) issued a Biological Opinion (BIOP) relative to the effects of the Klamath Project on the viability of Southern Oregon/Northern California Coast (SONCC) coho salmon in the Klamath River downstream from IGD (NMFS 2002). This evolutionary significant unit of coho salmon was listed as threatened by NOAA Fisheries in 1997 and by the State of California in 2002 (Federal Register 1997; CDFG 2002). The BIOP determined the operation of the Klamath Project jeopardized the existence of threatened SONCC coho salmon in the Klamath River and set forth a Reasonable and Prudent Alternative (RPA) to avoid jeopardizing their existence. Among the elements of the RPA were a prescribed regime of minimum flows at IGD and a water bank of 100,000 acre feet with implementation to be phased in over a 10-year period. The premise of these elements was that increased river discharge would speed migration of juvenile coho salmon through the Klamath River and result in increased survival. The National Research Council (NRC) noted that while this may theoretically be possible, there was no existing information to support this conjecture for Klamath River coho salmon (NRC 2001). In

response to the NRC report, the BIOP mandated the U.S. Bureau of Reclamation to implement several studies, including those to determine the extent that spring IGD flow regimes affect survivorship of juvenile coho salmon during their downstream migration. This study is an outcome of that mandate.

Factors affecting juvenile coho salmon migration, survival, and habitat preference during varying flow regimes of the Klamath River are largely unknown. The limited abundance of juvenile coho salmon within the main stem Klamath River and its tributaries preclude the use of traditional mark and recapture methods to study movement and survival (NMFS 2002). However, radio telemetry provides researchers with a powerful method of evaluating downstream migratory behavior and survival of fish populations where the ability to capture and mark large numbers of individuals is impaired (Hockersmith et al. 2003), and has been used to study juvenile salmon migration patterns (McCleave 1978; Berggren and Filardo 1993; Lacroix and McCurdy 1996; Giorgi et al. 1997; Hockersmith et al. 2003; Miller and Sadro 2003) and estimate survival (Skalski et al. 2001; Skalski et al. 2002) of several salmonid species.

Studies on various salmonid species on the Columbia and Snake rivers have provided evidence that the migration rate of juvenile salmon through impoundments is positively related to water velocity (Berggren and Filardo 1993; Giorgi et al. 1997), but little evidence of a link to survival has been found (Smith et al. 2002). Berggren and Filardo (1993) also identified water temperature and release date as key factors influencing migration rate. Muir et al. (1994) experimentally demonstrated the level of smoltification and migration rate could be influenced by water temperature and photoperiod. Smith et al. (2002) did not find a significant relation between river discharge and survival of yearling Chinook salmon and found only a weak relation in juvenile steelhead. However, the Klamath River is a much different system than the main stem Columbia and Snake rivers, and different processes may affect juvenile salmonids in the two systems.

The objectives of the present study were to: 1) provide estimates of the survival of hatchery and wild juvenile coho salmon downstream from IGD, 2) determine if there is a

relation between flow and other environmental and physiological variables with survival of juvenile coho salmon, 3) determine if there is a relation between flow and other environmental and physiological variables with migration of juvenile coho salmon, and 4) determine if juvenile hatchery coho salmon can serve as surrogates for wild fish for future survival studies.

METHODS

Study Area

The study area encompassed most of the lower 310 river kilometers (rkm) of the main stem Klamath River from IGD to the estuary near the mouth at the Pacific Ocean (Figure 1). Automated radio telemetry stations were located near the confluences of major tributaries and above the estuary. The reach from IGD (rkm 310) to the Scott River (rkm 234) is significantly influenced by IGD flow releases and was the primary focal area studied to address objectives 2-4 (Figure 2).

Transmitter specifications

Pulse-coded radio transmitters operating at 164.320, 164.480, 166.478, and 166.758 MHz were used. Transmitter dimensions were 5 mm wide by 3 mm high by 13 mm in length and weighed 0.43 g in air and 0.29 g in water (Lotek Wireless, Newmarket, Ontario, Canada; model NTC-M-2). The antenna (type S1) measured 0.3 mm by 16 cm and was covered in a Teflon coating. Within each frequency, transmitters were differentiated into five subgroups based on the burst rate of their uniquely coded radio signal (7.8, 7.9, 8.0, 8.1, and 8.2 s). The expected life of transmitters using a coded burst rate of 8 s was 45 d.

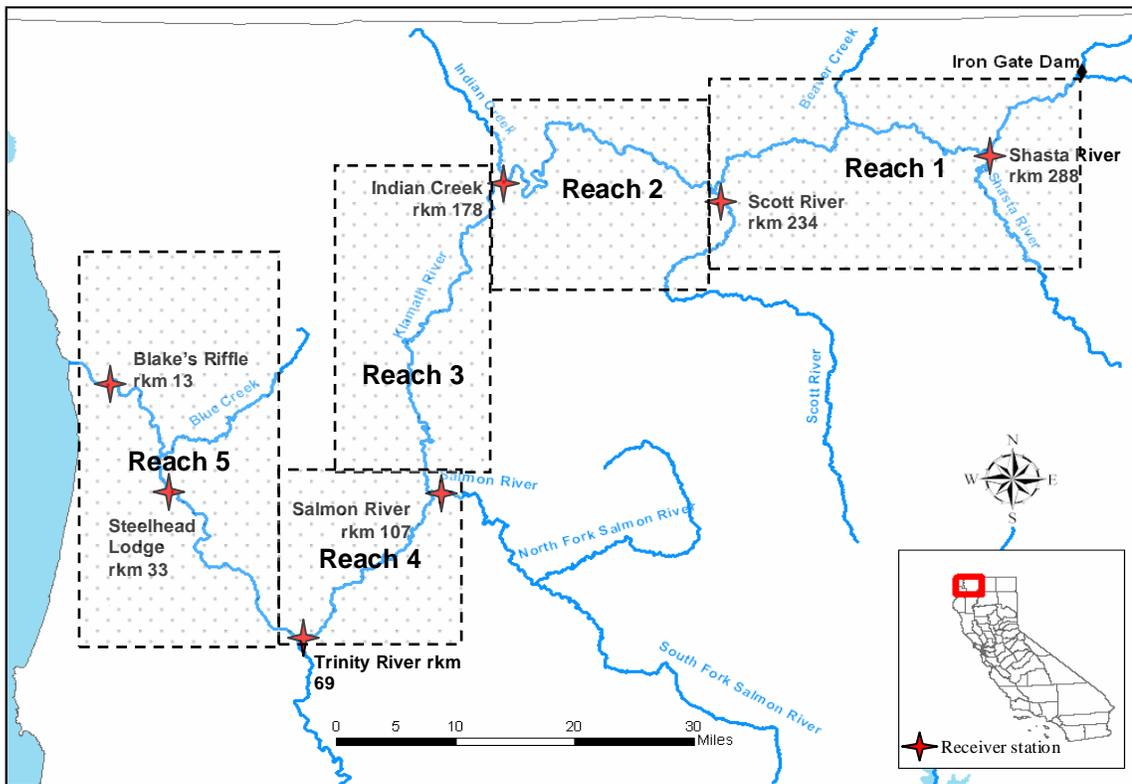


Figure 1. Map of the Klamath River study area showing tributaries of five index reaches and locations of automated radio telemetry stations deployed in 2006.

Stationary Detection Systems

Seven automated radio telemetry stations were established along the main stem Klamath River from IGD to near the upper estuary (Figure 1). The location and dates of operations of each station are listed in Table 1. Each station consisted of two three-element Yagi aerial antennas, mounted on a 4 m mast, connected to two data-logging receivers (Figure 3). Two types of data-logging receivers were deployed at each array (SRX-400, Lotek Wireless, Newmarket, Ontario, Canada; Orion, Grant Systems Engineering, Newcastle, Ontario, Canada) because each has unique operational characteristics that enhance the detection of radio tags. For example, SRX receivers are more sensitive and are better at detecting weak signals but have a longer scan cycle. Each receiver was configured to maximize the potential for detecting tagged fish. The SRX receivers monitored each frequency for 8.7 s before cycling to the next frequency. The

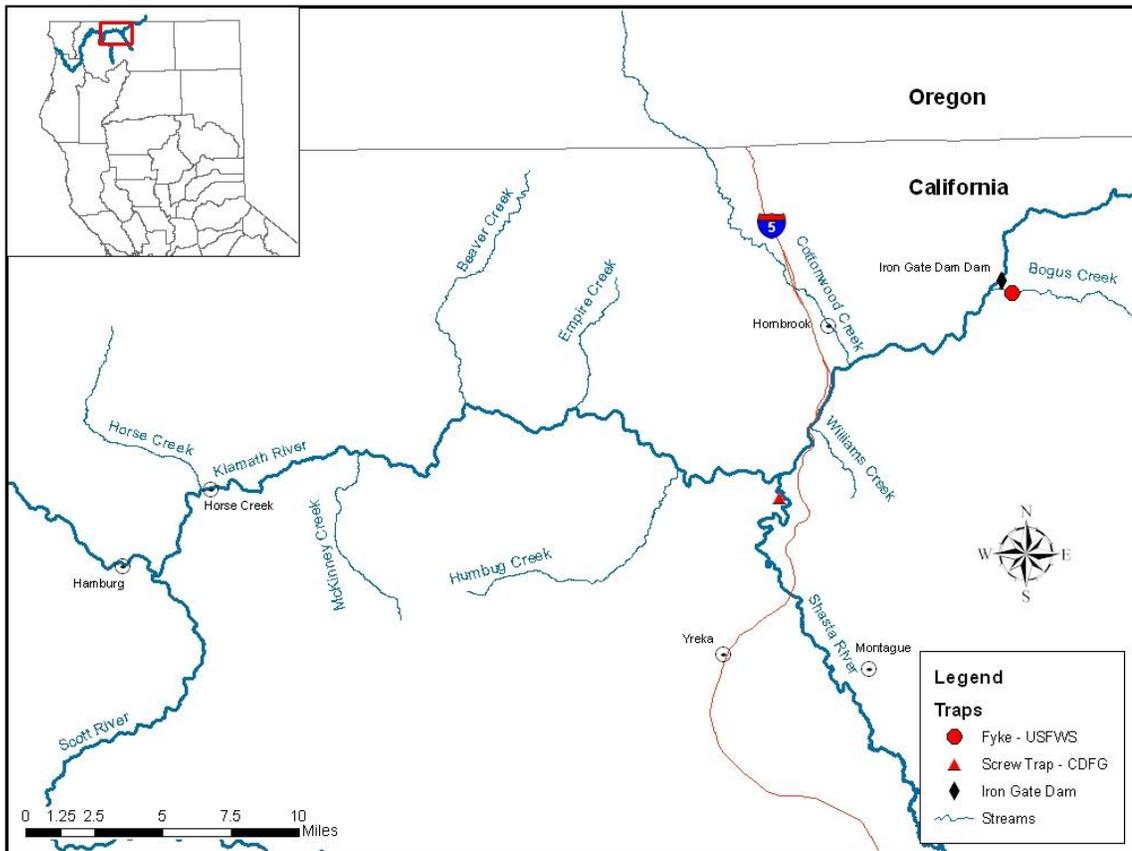


Figure 2. Upper main stem Klamath River study area and location of fish collection and tagging sites at Iron Gate Dam and the Shasta River.

Orion receivers are able to scan all of the frequencies at 164 MHz simultaneously and then switch to 166 MHz, allowing the Orion half the scan time of the SRX_400 receiver. Each array was supplied power by a 12V system (180 amp hour battery) powered by a 170 W photovoltaic bank. Receiver gain level was set to maximize signal reception while avoiding detection of erroneous signals caused by local interference (i.e., power lines, private radio transmissions). The gain of most SRX receivers was set near 75 on a unitless scale of 0 to 99. The noise floors of the Orion receivers were generally set near -120 dB. When a signal was detected, transmitter channel (frequency), code, signal strength, time, and date were recorded. Stations collected data continuously. Radio telemetry data were downloaded from each site weekly.

Table 1. Summary of automated radio telemetry stations deployment in 2006.

Site location / Flow reach	rkm	Receiver type	Dates of operation
Shasta River / Test	288	SRX-400 & Orion	3/22/06 – 7/21/06
Scott River / 1	234	SRX-400 & Orion	3/21/06 – 7/21/06
Indian Creek / 2	178	SRX-400 & Orion	3/21/06 – 7/21/06
Salmon River / 3	107	SRX-400 & Orion	3/20/06 – 7/12/06
Trinity River / 4	69	SRX-400 & Orion	3/20/06 – 7/21/06
Steelhead Lodge / 5	33	SRX-400 & Orion	3/19/06 – 7/21/06
Blake's Riffle / 5a	13	SRX-400 & Orion	3/19/06 – 7/21/06

Reach designations: (Test) IGD – Shasta R.; (1) IGD – Scott R.; (2) Scott R. – Indian Cr.; (3) Indian Cr. – Salmon R.; (4) Salmon R. – Trinity R.; (5) Trinity R. – Steelhead Lodge.; (5a) Trinity R. – Blake's Riffle.

Mobile Detection Systems

Mobile tracking was conducted to collect data from tags between the locations of automated receivers to aid in determining tag fate. This task was important because data from mobile tracking were used as an aid in proofing data from automated receiving systems and recovered tags were censored during migration analyses (see the Migration Analyses section for a further description of censoring).

Radio-tagged fish were located during weekly surveys by field crews equipped with Lotek SRX-400 receivers connected to three-element Yagi antennas from 19 April through 29 June 2006. Surveys were made from jet boats, automobiles, and rafts. All surveys were conducted during daylight hours.

Information about the location, habitat, and behavior were recorded when radio-tagged fish were located. A Global Positioning System (GPS) receiver (Garmin GPSMap



Figure 3. Typical automated radio telemetry detection station. This particular detection site is located approximately 1.5 km upstream of the confluence between the Klamath River and Indian Creek.

76S) was used to record spatial coordinates. Fish positions were then assigned the nearest river kilometer and Meso-Habitat Type unit (MHT) using aerial photographs of the river with this information superimposed over the image. Other information recorded each time a fish was located included, date, time, channel code (fish ID), and scaled ratings of movement and position relative to previous known positions. Assignment of movement ratings were based upon a minimum 5 min observation period at a maximum distance of approximately 5 m to the fish position.

Additional information was collected from transmitters having a remaining expected tag life of less than 10 d. Crews were provided instructions which included protocols for diving and the use underwater antennas constructed by stripping the sheath of coaxial cable to expose 10 cm of the center wire. Diving with these antennas allowed crews, under suitable conditions, to determine the exact location and recover transmitters that were no longer in fish.

Accuracy of recorded fish locations made during vehicle surveys varied because of several factors, including access limitations due to land ownership, topography, road location relative to river, fish position within the river channel, and streamside accessibility. Although not directly measured, accuracy of the recorded position in cases where fish could be approached directly was estimated to be as little as 5 m and was limited by the distance of the fish from shore and water depth. Accuracy of fish locations recorded during float surveys are generally greater than those made by vehicle due to maneuverability of the raft. Estimated detection distance ranged from < 1 m to more than several meters depending on water depth, velocity, and activity level of the fish.

Fish Handling and Tagging

Collection

Hatchery fish were obtained from the California Department of Fish and Game (CDFG) Iron Gate Fish Hatchery (IGH) and wild fish were collected from the rotary screw trap on the Shasta River operated by the CDFG. Wild fish used in this study were held on site in a floating net pen (1.2 x 0.61 x 0.61 m with a 5 x 5 mm bar mesh) for up to 3 d before being used in this study. A sub-group of 500 hatchery fish used for tagging were transferred from outdoor raceways into a large outdoor tank (2,256 L; 1.4 m width, 4.5 m length, 0.4 m deep) on 22 March 2006. This subgroup of fish was also used to carry out a gill ATPase experiment to determine the relationship between in river exposure time and gill ATPase activity (described later in this report).

Transport

Transporting fish was required to enable the paired-release design, which required two release sites. The goal of transportation was to subject control and treatment groups to similar conditions despite being transported to different locations. Hatchery fish in the control group were transported by vehicle downstream to the Shasta River before being tagged and released. Likewise, wild fish in the test group were transported upriver to the hatchery before being tagged and released. To ensure similar treatment of test and control groups, hatchery fish in the test groups and wild fish in the control groups were

transported by vehicle a distance equal to that experienced by their counterparts in opposite treatment groups. All fish were transported by vehicle in a 115 L oval-shaped tank with a battery powered re-circulating pump. Stress Coat® (Aquarium Pharmaceuticals Inc., Chalfont, Pennsylvania) was added to the tank (1 ml/10 L) prior to transport to reduce electrolyte loss and damage to skin tissue. Water temperature and dissolved oxygen were recorded (YSI Model 55 YSI Incorporated, Yellow Springs, Ohio) at collection sites, pre-transport, post-transport, and at holding sites to assure proper water quality conditions were maintained for holding and transporting fish. Prior to and during transport dissolved oxygen in the transport tank was maintained at a minimum level of 80% saturation using oxygen supplied through an air stone at 10 psi. Water temperature was maintained within 2°C of the collection source temperature during transport using dechlorinated ice when needed. If collection source and holding site water temperatures differed by more than 2°C, the transport tank water was tempered to within 2°C at a rate of 0.5°C/15 min. Following transport, fish were held at tagging sites within floating net pens (1.2 x 0.61 x 0.61 m with a 5 x 5 mm bar mesh) before being tagged that day (Figure 4).

Surgical Procedures

Procedures for surgical implantation of radio transmitters were similar to those described by Adams et al. (1998). A foam support with a center groove shaped to fit the dorsal surface of a small salmon was lined with a chamois soaked in PolyAqua® (Novalek, Inc., Hayward, California) to support the fish's body during surgery. Fish were placed into primary anesthesia solution (approximately 70 mg/L) of tricaine methanesulfonate (Fiquel® MS-222 (Argent Chemical Laboratories, Redmond, Washington)) until loss of equilibrium occurred. After removal from the primary anesthetic, each fish was placed ventral side up in the surgical support and the gills were flushed with a secondary anesthetic solution of tricaine methanesulphonate (20 mg/L) continuously administered at a rate of approximately 250 mL/min through a tube placed in the fish's mouth for the duration of the procedure. The mean (\pm 1SD) time to complete each surgical procedure was 2 min 48 s (\pm 23 s).



Figure 4. Holding pens at Iron Gate Hatchery, located at the entrance to the adult fish ladder. Photograph on right shows the bucket layout within each net pen. Photographs were taken on 19 April 2006.

Prior to insertion, transmitters were disinfected using a 0.5% disinfectant solution of chlorohexidine diacetate (Nolvasan® Fort Dodge Animal Health, Fort Dodge, Iowa). Transmitters were rinsed twice in sterile water and placed on the sterile portion of a surgical glove wrapper along with the surgical instruments immediately before surgery. Because complete sterilization of surgical equipment under field conditions is difficult, two sets of surgical equipment were alternately employed, enabling one set to be disinfected by soaking in the 100 percent ethanol while the other set of instruments was being used in surgery. Sterile surgical gloves were worn during each surgical procedure.

To implant the transmitter, a 7-mm incision was made approximately 5 mm anterior to the pelvic girdle and 3 mm away from and parallel to the mid ventral line. The incision made was only deep enough to penetrate the peritoneum (Summerfelt and Smith 1990). The shielded-needle technique described by Ross and Kleiner (1982) was used to provide an outlet through the body wall for the transmitter antenna. A 16-gauge x 133 mm catheter-covered needle (BD Angiocath I.V.) was inserted through the incision and guided 10-15 mm posterior and slightly caudal to the pelvic girdle. After depressing the needle through the body wall, it was removed through the incision, leaving the nylon

catheter tube to guide the transmitter antenna through the body wall. The antenna of the transmitter was then fed through the incision end of the catheter and pulled out the exiting end as the transmitter was inserted into the body cavity. The transmitter was positioned to lie slightly posterior to the incision by gently pulling on the antenna. A single simple interrupted suture (Ethicon coated vicryl braided, 5-0 reverse cutting P-3 needle) closed the incision. After suturing, a small amount of antibacterial ophthalmic ointment (Neobacimyx®) was spread over the incision site to reduce the risk of infection (Summerfelt and Smith 1990).

Only coho salmon weighing 8.6 g or greater were tagged to ensure the transmitter weight did not exceed 5% of the individual's body weight (Adams et al. 1998). Transmitters represented between 0.6 and 3.6 % of the body weight of fish used in the study. Juvenile coho salmon radio-tagged each day were held in a floating net pen (1.2 x 0.61 x 0.61 m) on site for approximately 24 h (range 20–33 h) before being released after dark.

Measures of Smoltification and Disease

Gill ATPase Activity

A non-lethal sample of gill tissue was collected prior to surgical implantation of the radio transmitter to assess the relationship between smoltification and migration rate or survival. The Na⁺-K⁺ gill ATPase activity level in the gill sample was quantified and used as a measure of smoltification. The small piece of gill filament (about 2 x 3 mm) was removed from the first gill arch on the left side and was suspended in a sample tube containing 0.5 mL of buffer solution, following the methods described in Schrock et al. (1994). Sample tubes were placed directly into liquid nitrogen, and then later stored at -80°C until processing. Each sample tube was uniquely labeled to identify the fish sampled.

An experiment based on untagged hatchery fish was conducted to determine if ATPase activity changed after fish were transferred from the hatchery to the Klamath

River. A group of 70 hatchery fish were selected at random from a pool group of approximately 500 fish held at IGH. These fish were transferred to in-river net pens, and gill samples were collected from 10 fish at each of 0, 1, 3, 6, 10, 14, and 21-d post transfer. To capture the wider range of environmental conditions, the experiment was conducted twice throughout the study, with the first trial occurring from 19 April to 10 May 2006 and the second from 16 May to 30 May 2006. The gill ATPase activities in samples collected throughout the study period were later determined by Biotech Research and Consulting, Inc. (Corvallis, Oregon) using the methods described in Johnson et al. (1977) for a whole homogenate assay.

Bacterial Kidney Disease

Although juvenile salmonids in the Klamath River are known to be infected with various diseases and parasites, e.g., *Ceratomyxa shasta*, *Parvicapsula minibicornis*, and *Renibacterium salmoninarum*, most testing has been restricted to juvenile Chinook salmon. Little is known about the prevalence of infections in other salmonids, including juvenile coho salmon. Because it could be important to know the prevalence and severity of diseases in coho salmon and the influence of the diseases on migration rate and survival we sampled for *R. salmoninarum*, the causative agent of Bacterial Kidney Disease (BKD), using a non-lethal sampling method. *Renibacterium salmoninarum* can be detected in small gill tissue samples thus avoiding the mortality associated with collection of kidney tissue. Tissue collection was limited to non-tagged hatchery coho salmon at IGH.

Hatchery coho salmon were randomly netted from the tank holding fish for the radio-telemetry objective for BKD testing on 24 May 2006. After each fish was anesthetized, a small sample of gill tissue (approximately 2 x 3 mm) was removed from the first gill arch. The tissue sample was placed in a pre-weighed cryotube and immediately placed in liquid nitrogen for preservation. Dissecting scissors and gloves were replaced between each sampling event to prevent cross contamination. Samples were analyzed by U. S. Geological Survey, Western Fisheries Research Center, Seattle, Washington, following the methods described in Chase et al. (2006).

Data Analyses

Converting Radio Signals into Detection Histories

Radio telemetry data from automated detection arrays were converted into detection histories to calculate detection probabilities specific to each array. The automated arrays recorded more than 2,000,000 radio signals that were processed to create reliable detection histories before analyzing fish detection data. These signals included multiple detections from live fish, potentially dead fish, as well as spurious signals. The purpose of signal processing was to segregate true detections of radio-tagged fish from spurious records.

Valid detections were identified by filtering radio signal data using multiple data proofing criteria. Raw release and automated detection array data were merged and proofed against five criteria using a program written in the SAS programming language (version 8.1; SAS Institute Inc., Cary, North Carolina; Figure 5). Records that did not meet the automated criteria were examined independently by staff at the USGS and USFWS offices and reconciled to determine their validity. An additional 10 % of the records passing the criteria were examined manually as a quality control measure to ensure the automated process was performing satisfactorily. After reconciliation, a final database was created for use in analyses.

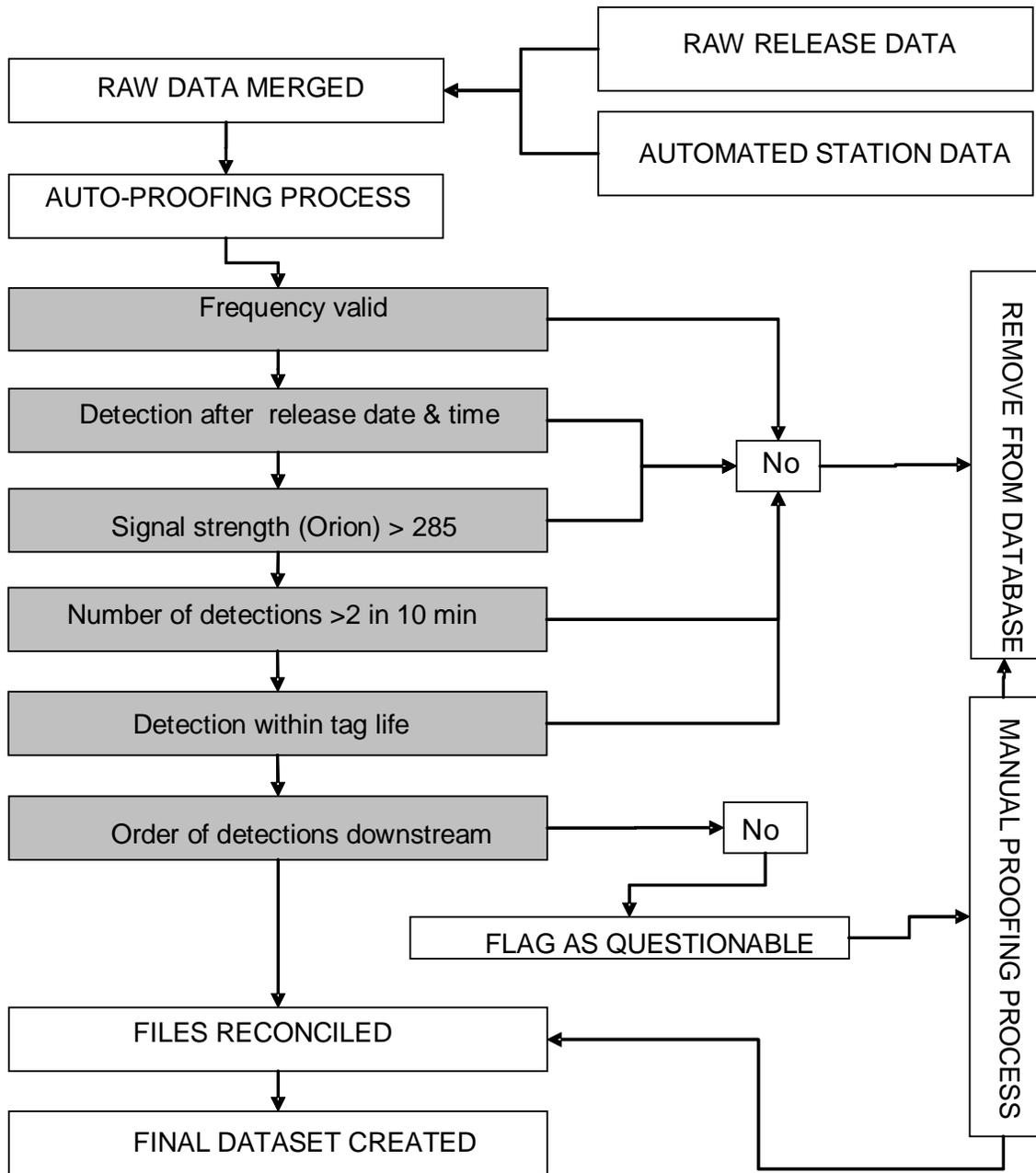


Figure 5. Project data flow and criteria used to identify valid radio signals recorded at radio telemetry stations. Shaded boxes represent automated data filter criteria.

River Conditions

Daily average river discharge values were obtained from monitoring stations operated by the U. S. Geological Survey at points along the main stem Klamath River and its tributaries. The method for quantifying the discharge experienced by a radio-tagged fish as it migrated through index flow reaches differed within each reach depending on the location of main stem and tributary flow gauges (Table 2). Temperature data were collected at 5 min intervals using Onset Stowaway[®] TidbiT[®] temperature data loggers (range 4–38 °C) placed within the main stem Klamath River directly above tributaries delineating the end of index flow reach boundaries and at the net pens we used to hold fish prior to release.

Table 2. USGS gauge descriptions and calculation methods used to quantify river discharge within index flow reaches during the 2006 study period.

Reach	Gauges used	Calculation
Test	IGD	None
1	IGD, Scott R., Seiad	(Seiad - Scott) + (IG)/2
2	Seiad	Seiad
3	Seiad, Indian Cr., Salmon R., Orleans	(Orleans - Salmon) + (Seiad + Indian Creek)/2
4	Orleans	Orleans
5	Orleans, Trinity R.	(Trinity + Orleans)
5a	Orleans, Trinity R., Blake's Riffle	(Trinity + Orleans) + (Blake's Riffle)/2

Reach designations: (Test) IGD – Shasta R.; (1) IGD – Scott R.; (2) Scott R. – Indian Cr.; (3) Indian Cr. – Salmon R.; (4) Salmon R. – Trinity R.; (5) Trinity R. – Steelhead Lodge.; (5a) Trinity R. – Blake's Riffle. USGS gauge sensor ID numbers: IGD (11516530); Shasta R. (11517500); Scott R. (11519500); Seiad (11520500); Indian Cr. (11521500); Salmon R. (11522500); Orleans (11523000); Trinity R. (11530000); Blake's Riffle (11530500).

Migration Analyses

Migration was examined primarily using time-to-event analysis methods. These methods are designed for the analysis of the occurrence of the timing of events. They are commonly used in the health field to evaluate the effects of treatments on death rate, and hence they are often referred to as methods for “survival analysis”. As such, much of the terminology within these methods stems from their use in the medical field and can be confusing in other fields (e.g., survivor functions). Their general use is well described in

the literature (Muenchow 1986; Pyke and Thompson 1986; Hosmer and Lemeshow 1999), but their use to describe fish movements was first described by Castro-Santos and Haro (2003). The methods are particularly suited to analysis of times until events occur because they allow for censoring (i.e., removal of an observation of an individual from analysis after some point, but using its data beforehand) and analyses of time-dependent variables. An example of censoring would be to omit observations of an individual from analyses after it was known to have died, or its radio transmitter was found separated from the fish. Time-dependent variables include river discharge and temperature, which change between detection sites over time.

The survivor function was used to compare the distributions of event times between groups or origins within reaches. The survivor function of a variable T is defined as:

$$S(t) = \Pr\{T > t\}$$

where T is a random variable with a probability distribution, denoting an event time for an individual. If the event of interest is passing through a reach of river, the survivor function gives the probability of not passing the terminus of the river reach of interest after time t . As such, the median time occurs when the survivor function equals 0.5. Survivor functions were estimated using the Kaplan-Meier method, in which the time-interval boundaries are determined by the event times and censored observations are assumed to be at risk for the entire event period. The alternative is the Life Table method, in which the time interval boundaries can be specified by the analyst and censored data are censored at the midpoint of the time interval (Hosmer and Lemeshow 1999). Survivor functions were plotted and compared between fish groups (treatment or control) and origins (hatchery or wild). Comparisons of survivor functions between groups and origins were made using Log-Rank and Generalized Wilcoxon Rank Sum tests (Allison 1995; Hosmer and Lemeshow 1999). Tests were conducted to compare origins controlling for group and group controlling for origin within each reach. In our analyses the ‘event’ was passing the downstream end of the river reach of interest and the ‘time to the event’ was the time from the last detection at the upstream end of the reach

(or the release time in the case of Reach 1) to the first detection at the downstream end of the reach, i.e., the travel time.

The relation between selected covariates and fish travel time was assessed using Cox Proportional Hazards regression analysis. In these analyses the effects are written in terms of the hazard function. The hazard function is defined as:

$$h(t) = \lim_{\Delta t \rightarrow 0} \Pr\{t \leq T < t + 1 \mid T \geq t\} / \Delta t$$

and is the instantaneous risk that an event will occur at time t . The equation describes a conditional rate: it is the ‘probability of the event time occurring in a limited time interval, conditional on the event having not occurred yet’, divided by the length of the interval (which makes it a rate, not a probability; Allison 1995).

The Cox proportional hazards regression model was used to examine the effects of several time-independent and time-dependent variables and their interaction terms when appropriate. The data were examined to ensure model assumptions of linearity and proportional hazards were met and correlations between variables were examined to determine autocorrelation. Linearity was assessed visually by plotting the Martingale residuals and by including dummy variables for several values of each predictor variable in regression models and plotting the resulting slope parameter estimates over the discrete values of the variable. The proportional hazards assumption was assessed statistically by including interactions of each variable with the mean-centered log of time in a regression model and examining the significance of their slope parameter estimates using the Chi-Square statistic (Hosmer and Lemeshow 1999). Covariates included in the models were initially selected by applying logical subject-matter knowledge and were removed based on the significance of their slope parameter estimates. Variables included as main effects included origin, group, river discharge, river water temperature, ATPase, fish weight, and serial date of release. Interactions of several of these variables were also added to the full models (i.e., most parameterized). The daily average values of the main effects of river discharge and water temperature were used as time-dependent covariates. The full

models were reduced to their final form by omitting variables one at a time in descending order of the Chi-Square P -value until the slope parameters of the remaining variables were all significant. Model selection was also assessed using Akaike Information Criterion (AIC) and AIC weights as described in Burnham and Anderson (1998). Robust sandwich variance estimates were used based on grouping fish into release cohorts by origin and release date. This method adjusts the estimates of the variance of the model coefficients to account for correlation among related observations, such as those released on a common date (Hosmer and Lemeshow 1999). An overall goodness of fit test was performed comparing the final models to those with an additional 10 dummy variables as described in Hosmer and Lemeshow (1999).

We chose to use the Cox proportional hazards regression methods to determine which variables, if any, were significant predictors of travel time through the reaches examined, but did not focus on the hazard ratios to explain their effects. The interpretation of the hazard is based on the risk of an event occurring, and is not directly related to the differences in time to an event of two groups, such as the travel time of hatchery and wild fish. In addition to the slope parameter estimates, we used time-based differences in predicted survivor functions from the models (i.e., differences in predicted median time to travel through a reach) as measures of the effects of significant predictor variables, as this time-based method is generally more intuitive (Spruance et al. 2004).

Survival Analyses

The basis for estimating survival using mark-recapture methodology is described by Burnham et al. (1987). Methods to accommodate specific issues related to the use of radio telemetry are described by Burnham et al. (1987) and Skalski et al. (2001) and their methods have been used successfully in a variety of studies (Counihan et al. 2002, 2005; Skalski et al. 2002).

Apparent survivals were estimated based on Cormack-Jolly-Seber capture-recapture methods (Cormack 1964; Jolly 1965; Seber 1982). Apparent survival is the probability that an animal remains available for recapture. In the context of this study, it is the joint

probability that the animal is both alive and migrates through the study area. As such, fish that stop migrating, or travel to areas outside the main stem Klamath River and do not return during the study are counted as mortalities. Fish remaining within the study area after their transmitters cease operating are also counted as mortalities. All references to ‘survival’ estimated during this study refer to apparent survival. Inasmuch as detection at a site is the product of the probability of survival to the site and the probability of capture at the site, these parameters must be separately estimated. The assumptions associated with the method depend on the design of the experiment and are described below.

The analyses were carried out within the program MARK (White and Burnham 1999). The process included assessing model fit, building a series of *a priori* models based on subject matter knowledge, ranking the models on the basis of parsimony using the AIC or one of its variants, assessing model uncertainty and using model averaging where appropriate, and producing estimated apparent survivals (ϕ , Φ) and capture probabilities (p). Model fit was assessed using the median \hat{c} procedure (Cooch and White 2006). When appropriate, adjustments to AIC were made for small sample sizes relative to the number of parameters in the models (AICc), to account for extra-binomial variation (QAIC), or both QAICc. Detailed descriptions of these methods can be found in White and Burnham (1999) and Burnham and Anderson (1998).

Single-Release Design

The single-release design was used to estimate survival of fish through the various study reaches and over them all. The term “single-release” refers to the use of one or more releases of fish made at a single location. This design requires as a minimum the following elements: that tagged fish are uniquely identifiable, at least two downstream detection sites exist below release locations, the re-release of all or some of the marked fish recaptured at each detection location, and the recording of the identity of the marked fish recaptured at each location (Peven et al. 2005). John Skalski (University of Washington) in Peven et al. (2005) provides a discussion of the potential biases associated with this and other designs. The primary potential bias associated with this

design is that expression of mortality due to tagging or handling cannot be separated from other sources of mortality. These can be separated using the paired-release design, which is described later in this section.

Survival can be estimated from the release point to the next detection site and from then on, survival is estimated from the detection zone of one detection site to the next. Unique recapture probabilities can be estimated at both sites bounding each reach except the last reach (see schematic in Figure 6). In the last reach, only the joint probability of survival to, and being detected at, the last site can be estimated (i.e., $\lambda = \Phi \cdot p$). Thus, the minimal study design must consist of at least two downstream detection locations. The assumptions of the single-release design are the following:

- A1. Individuals marked for the study are a representative sample from the population of interest.
- A2. Survival and recapture probabilities are not affected by tagging or sampling. That is, tagged animals have the same probabilities as untagged animals.
- A3. All sampling events are “instantaneous.” That is, sampling occurs over a negligible distance relative to the length of the intervals between sampling locations.
- A4. The fate of each tagged individual is independent of the fate of all others.
- A5. All tagged individuals alive at a sampling location have the same probability of surviving to the next sampling location.
- A6. All tagged individuals alive at a sampling location have the same probability of being detected at that location.
- A7. All tags are correctly identified and the status of each fish (i.e., alive or dead) is correctly assessed.

The first assumption (A1) involves inferences from the sample taken to the target population. For example, if inferences are desired for juvenile SONCC coho salmon, then the sample of tagged fish should be drawn from that population. These assumptions could be violated if the fish selected for tagging were on average larger than the target population, or if they had a substantially different migration pattern.

Assumption (A2) again concerns making inferences to the target population (i.e., untagged fish). If tagging has a detrimental effect on survival, then survival estimates from the single release-recapture design will tend to be negatively biased.

The third assumption (A3) stipulates that mortality is negligible immediately near the sampling arrays, so that the estimated mortality is associated with the river reaches and not the sampling event. For migrant salmonids, the time spent near detection equipment is typically brief relative to the time spent in the river reaches and the detection areas are small relative to the reaches between them.

The assumption of independence (A4) suggests that the survival or death of one fish has no effect on the fates of others. In a riverine situation this is likely true. Violations of assumption (A4) may bias the variance estimate (true variability would be greater than estimated).

Assumption (A5) specifies that the prior detection history of the tagged fish does not affect subsequent survival. The lack of handling following initial release of radio-tagged fish minimizes the risk that subsequent detections influence survival.

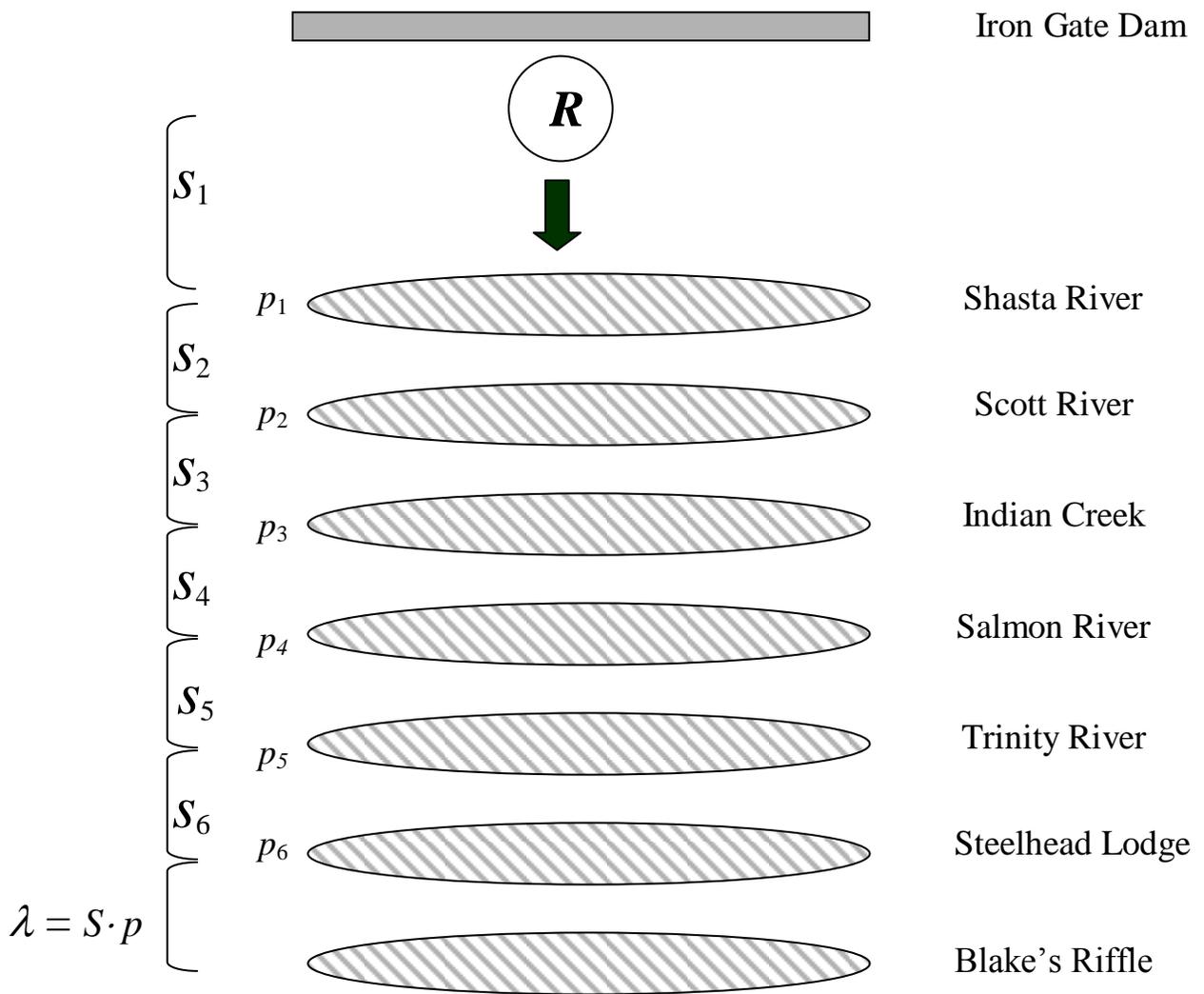


Figure 6. Schematic of release, possible detection sites, and estimated survival parameters (S = survival estimate, p = capture probability, and $\lambda = S \cdot p$) generated in a single release-recapture design to estimate juvenile coho survival from release (R) downstream from Iron Gate Dam through several reaches of the Klamath River. Ovals represent potential detection sites. Survival from any two points is the product of the survivals between the two points (e.g., survival from release to Indian Creek = $S_1 * S_2 * S_3$). Only λ , the joint survival and capture probability can be estimated in the last reach. The design applies to releases of hatchery and wild coho salmon.

Similarly, assumption (A6) could be violated if downstream detections were influenced by upstream passage routes taken by tagged fish. Violation of this assumption is minimized by designing telemetry detection fields that span the breadth of the river.

Assumption (A7) implies that fish do not lose their tags and are subsequently misidentified as non detected or dead fish are falsely recorded as alive at detection locations. Tag loss and tag failure would result in a negative bias (i.e., underestimation) of fish survival rates. The possibility of tag failure will depend on travel time relative to battery life. Dead fish drifting downstream could result in false-positive detections and upwardly bias survival estimates. Two actions were undertaken to determine if we met this assumption: data from a tag-life trial was compared with the time fish were in the study areas (Appendix 1) and euthanized radio-tagged fish were released. A sub-sample of radio-tagged fish were euthanized and released at both test and control sites. A total of 28 radio-tagged hatchery coho salmon (16 test and 12 control) were euthanized and released throughout the study period. Fish to be euthanized were randomly selected from the release group immediately prior to release.

Single-release-recapture methods were used to estimate an overall survival in each reach and among all reaches. In this analysis the results of the most likely model were used to estimate survivals and confidence intervals for each reach. The overall survival from release to the second to last capture site was estimated as the product of each reach estimate ($\Phi_{\text{overall}} = \Phi_1 * \Phi_2 * \Phi_3 * \Phi_4 * \Phi_5$, with variance calculated using the delta method (Seber 1982).

Model fit was assessed by plotting deviance residuals and overdispersion was assessed based on the most parameterized model. The program MARK provides several means to assess model fit; we chose to use the median c-hat procedure, because high capture probabilities resulted in many incalculable chi-square tests in the Test 2 and Test 3 goodness of fit methods of Burnham et al. (1987), rendering the overall Test 2 and Test 3 goodness of fit method unsatisfactory. Models were developed based on origin (hatchery, wild) and experimental group (control, treatment).

Paired-Release Design

The paired-release design was used to estimate survival from release near IGD to the Shasta River, without the potential effects of tagging and handling. The results are the apparent survival of test group fish released near IGD as a ratio, or relative, to those of control fish released near the Shasta River. The paired-release design has the advantage of incorporating potential tagging and handling effects, thereby yielding an unbiased estimate of reach survival. As such, the result of this design represents the survival between the release site of the test group to the release site of the control group, without the potential effects of tagging and handling. The model requires as a minimum two release locations and at least one downstream detection site. In addition to the assumptions required for the single-release design, the paired-release design requires:

A8. Survival in the lower river segment of the first reach is conditionally independent of survival in the upper river segment (i.e., $S_{t1} = S_{t_a} * S_{c1}$ and $S_{t_b} = S_{c1}$; see Figure 7).

A9. Releases R_t and R_c have the same probability of survival in the lower segment of the reach they share in common (between the release location of R_c and the first detection location; i.e., $S_{tB} = S_{c1}$ in Figure 7).

Use of the paired-release design does not necessarily prevent estimating survival downstream of the reach of interest using the single-release design. Figure 7 depicts a schematic of the paired-release design and estimable parameters. Figure 8 illustrates the concept of canceling out tagging and handling effects using the paired-release design.

The paired-release design was used to estimate the survival of the treatment group relative to the control group and to determine if tag and handling effects were present. A series of models was developed in which Φ and p were allowed to vary across groups or be constant across groups similar to that described in Burnham et al. (1987). For example, one model could allow Φ of treatment and control groups to vary in the first

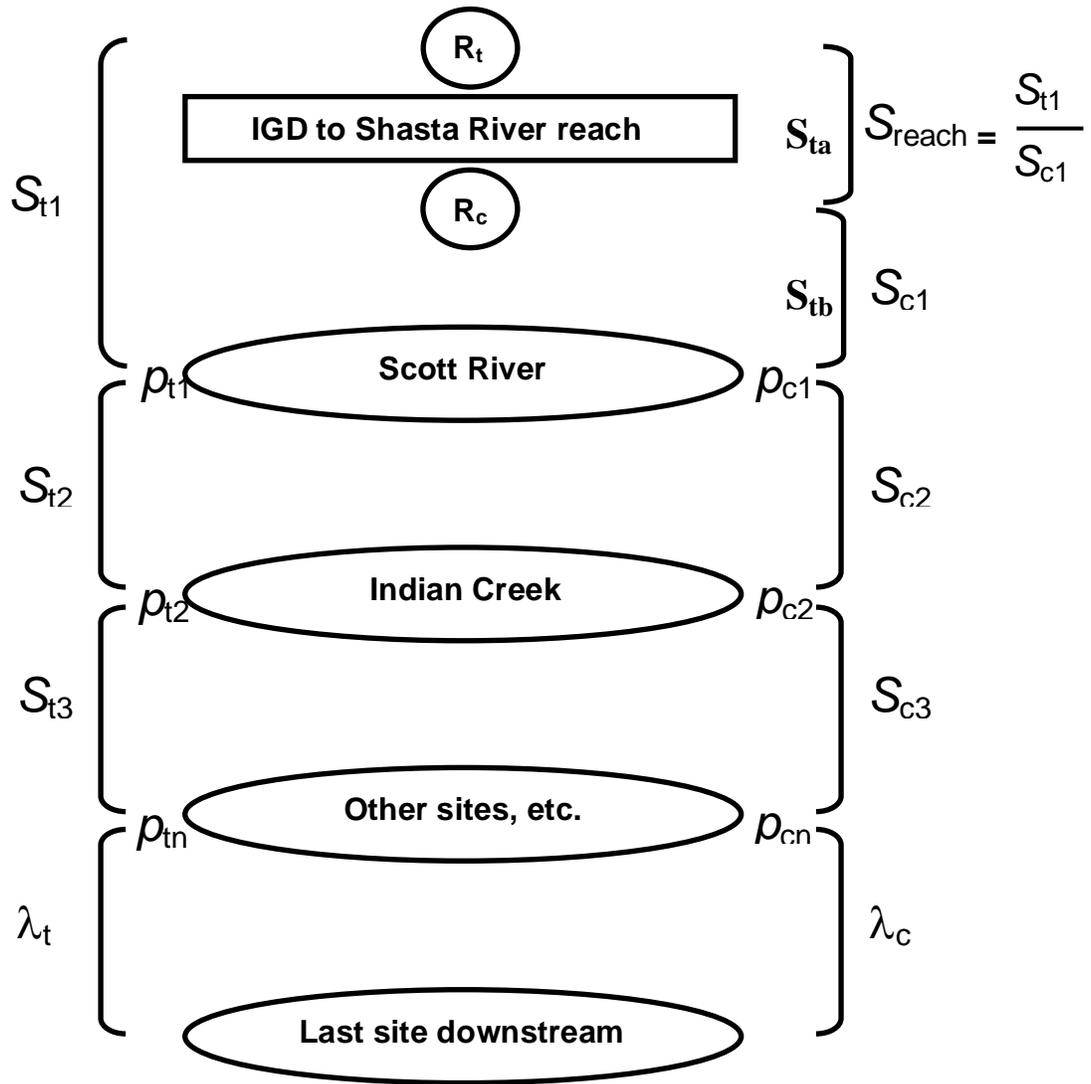


Figure 7. Schematic of a potential paired-release-survival model for the Klamath River juvenile coho salmon study. Test fish released near Iron Gate Dam (IGD) would be paired with control fish released near the detection site at the Shasta River to coincide with the passage of the test. The location of the control fish release is based on the definition of the reach of interest; the Shasta River was used for this example. Survival from release near the dam to the Shasta River (S_{reach}) would be measured relative to the control groups released near the Shasta River (R_c), canceling out effects of survival due to tagging and handling (see Figure 8). Survival from there to and between the other sites, other than the last one, can be estimated as well, with the method depending on the assumptions that can be satisfied. Only the joint probability of capture and survival (λ) can be estimated in the last reach.

$$S_{\text{reach}} = \frac{S_{t1}}{S_{c1}} = \frac{\text{M}_{\text{natural A}} \text{M}_{\text{natural B}} \text{M}_{\text{Tag}}}{\text{M}_{\text{natural B}} \text{M}_{\text{Tag}}}$$

Figure 8. Conceptual representation of how tag effects can cancel out within the paired-release design. Survival of the test group in the reach between release and recapture (S_{t1}) is affected by natural mortality in the reach between release of the test and control group (M_{Natural A}), from there to the detection site (M_{Natural B}) and tag and handling effects (M_{Tag}). Survival of the control group (S_{c1}) is affected by natural mortality between release and detection (M_{Natural B}) and tag and handling effects (M_{Tag}). All effects except M_{Natural A} cancel out in the ratio of S_{t1} to S_{t2} , resulting in an unbiased (S_{reach}) when model assumptions are met. See Figure 7 for a schematic of the paired-release design.

reach (i.e., an acute treatment effect), but be the same in all other reaches, and an alternative model could specify they are the same in all reaches (i.e., no treatment effect).

The models were ordered in terms of parsimony using the program MARK (White and Burnham 1999). The models were ranked according to a variant of the AIC and assessed based on their place in the ranking. Adjustments to AIC were made for small sample sizes relative to the number of parameters in the models (AIC_c). Results were generated after multimodel averaging based on model weights, because several models were supported. The methods for this approach are described in Burnham and Anderson (1998). The averaged models were used to generate estimates of Φ_{ti} and Φ_{ci} from which the relative survival estimate $S_i = (\Phi_{ti} / \Phi_{ci})$ was derived, where $i = 1$ to n denoting each of the study reaches. The 95% confidence intervals were calculated as ± 1.96 standard errors (SE), where the variance was calculated using the delta method (Seber 1982).

These methods were applied to fish of hatchery and wild origin separately. In this approach, the relative survival in the first reach (S_1) includes survival from the release site of the treatment group (IGH) to the release site of the control group (Shasta River), with tag and handling effects factored out (assuming these effects are expressed by the time of detection at the Scott River). This assumption was assessed by estimating

relative survivals in subsequent reaches; it was assumed to be violated if the 95% CI of these relative survivals did not overlap one.

Assessing impacts of covariates on survival

The effects of several individual and group covariates on apparent survival were assessed using the program MARK. Covariates were added to the most supported model from the single-release analyses and their effects were determined by examining the rank of the new models in the suite and the sign, size, and standard errors of their beta coefficients describing the covariate effect (i.e., slopes). The effects of the covariates: 1) Klamath River water temperature near the Scott River, 2) IGD discharge, and 3) release date were separately assessed by comparing models describing four hypotheses. The hypotheses included covariate effects in: 1) only the first reach (release to Scott River; Acute effect), 2) all reaches except the first (Scott River to rkm 33, Chronic effect), 3) all reaches (release to rkm 33, Acute + Chronic effect), and 4) no covariate effect (Time Only). These were chosen based on results from the migration analyses, which indicated fish spent much of their total time in the first reach, and the knowledge that the impact of IGD discharge diminishes as accretions from tributaries are added. Analyses were based on two data groups: hatchery and wild origin fish released on similar dates (25 April through 16 May 2006), and hatchery origin fish from the full set of release dates (4 April through 24 May 2006). The support for the hypotheses was assessed by comparing model weights among the four models of each covariate.

Quality Assurance measures

Prior to the field season activities a quality assurance (QA) plan was created to ensure that all field procedures and scientific data collection followed established protocols. The scope for this QA plan encompassed pre-season activities (planning), field activities (tagging/releasing), and office activities after data collection such as data processing, analysis, and preparation of the final report.

Before the field season began all personnel tasked with duties involving the creation or retrieval of data were required to review pertinent standard operating procedures (SOP) related to assigned tasks. When field activities began in April, a designated person monitored daily tasks to ensure all procedures conformed to written guidance. Periodic spot checks were done throughout the field season to ensure procedures continued to be followed.

Data collected (except automated detection data) was first hand-written, then at the earliest opportunity, entered into an electronic spreadsheet. The electronic spreadsheet was then visually proofed twice to ensure accuracy, before an electronic copy was sent to USGS and USFWS offices. At the USGS office, 10% of the data lines were randomly selected for another visual proofing before the electronic data were finalized and uploaded into the database. Discrepancies found during random line proofing were communicated back to the field staff for reproofing of entire datasheet. After the additional proofing, data were resubmitted for uploading. The automated detection data files were also subjected to proofing for completeness and file naming accuracy with 10% randomly selected prior to finalization. All quality assurance documents, copies of all hand-written data, and data files selected for proofing were stored with the 2006 Klamath River QA plan for later review.

RESULTS

River conditions

River discharge during the spring of 2006 was greater than the majority of recorded river discharge values for the period of record (1962-2005; Figure 9). During the 2006 study period, the average daily discharge at IGD (rkm 310) ranked 5th or higher for the period of record, with a mean of 3,956 cfs (range 997 and 10,300 cfs). Similarly, the average daily discharge recorded at Blake's riffle (rkm 13) ranked within the top eight of all observations for the period of record, with a mean of 25,789 cfs (range 4,740 to 50,600 cfs). Daily discharge data were obtained from <http://waterdata.usgs.gov/nwis/dv>.

The probability of river discharge exceeding values recorded at IGD, Seiad Valley, and Blake's Riffle during the 2006 study period was less than 0.20 for the months of April – July, and less than 0.5 at IGD during June and July (Figure 10). The contribution of IGD discharge to total river discharge volume was quite pronounced within the uppermost three flow reaches during the 2006 study period. From the dam downstream to Seiad Valley, the proportion of IGD discharge relative to total river volume was greater than 0.3 from April – July, 2006 (Figure 11).

Water temperature in the Shasta River (site of our control group holding pens) was elevated throughout most of the tagging period compared to temperatures of the main stem Klamath River directly above the Shasta River confluence (Figure 12). Water temperatures in the main stem Klamath River generally decreased downstream along the longitudinal gradient, due largely to accretions of colder water from tributaries. River discharge and water temperature were inversely correlated within all flow reaches during the 2006 study period (Pearson correlation coefficient; $|r| > 0.88$, $P < 0.001$, Figure 9).

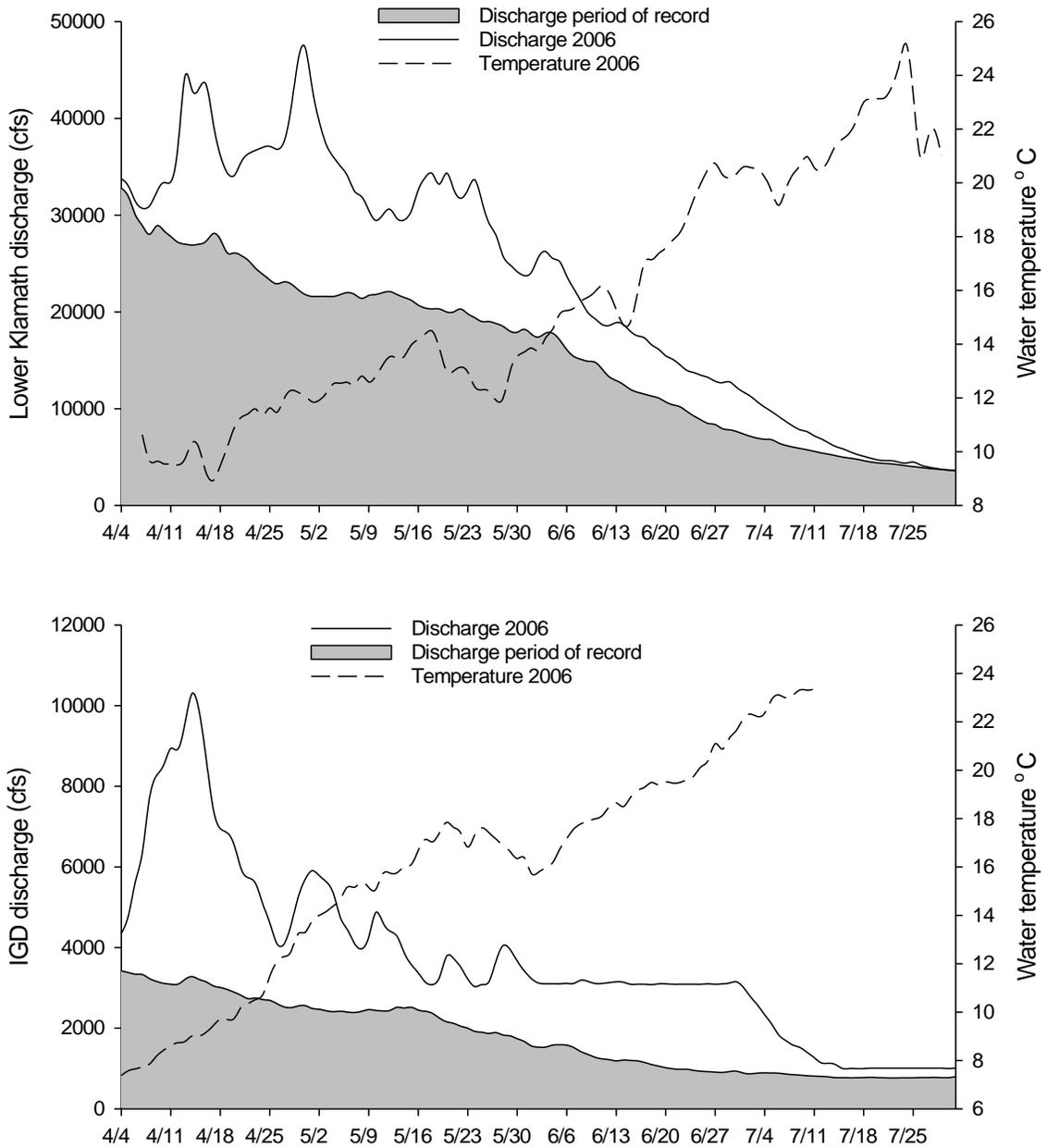


Figure 9. Mean daily discharge for period of record (1962-2006), and mean daily discharge and water temperature recorded at Blake’s Riffle (top figure; rkm 13) and Iron Gate Dam (bottom figure; rkm 310) during the 2006 study period.

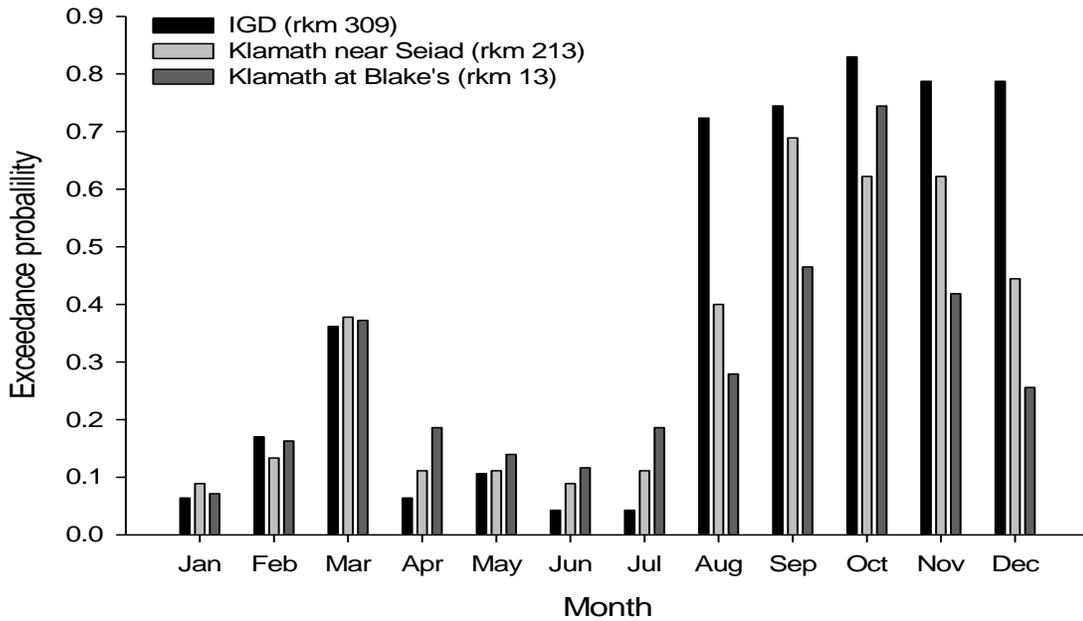


Figure 10. Exceedance probabilities of river discharge values observed during 2006 at Iron Gate Dam (IGD), Klamath River near Seiad Valley, and Klamath River near the estuary (Blake’s Riffle). Exceedance probabilities calculated using river discharge values for the period of record (1962–2006).

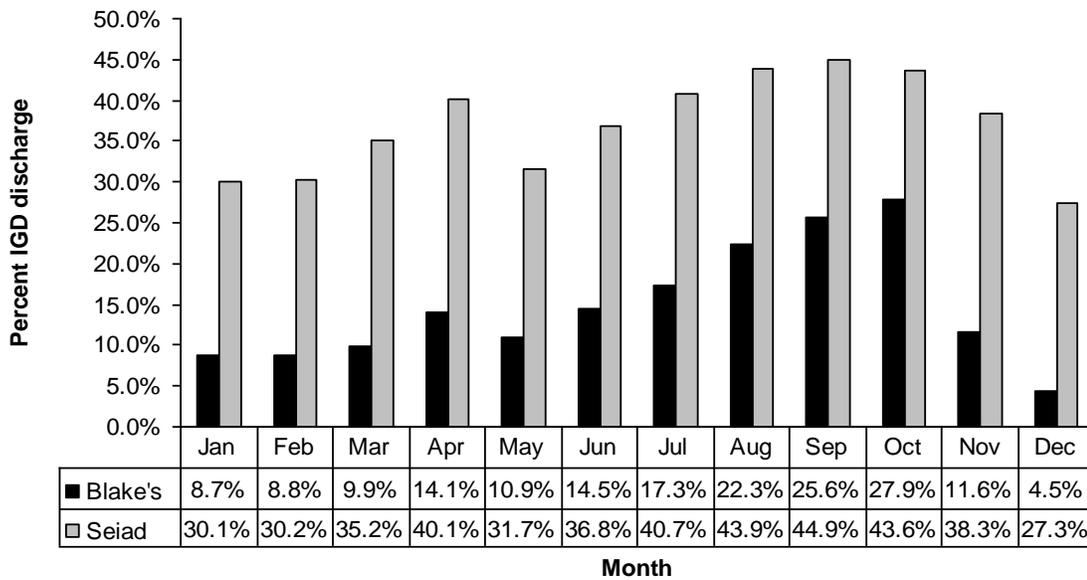


Figure 11. Proportion of discharge from Iron Gate Dam (IGD) relative to total river discharge at Seiad Valley (rkm 213) and at Blake’s Riffle (rkm 13) during 2006.

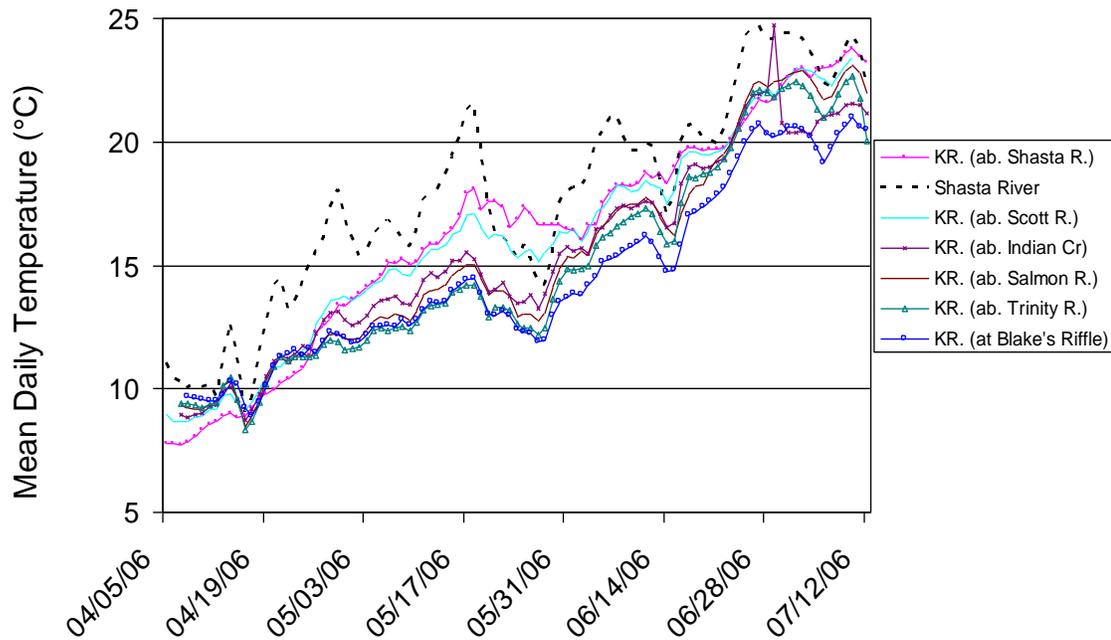


Figure 12. Mean daily water temperatures (°C) during the study period in 2006. Temperatures were measured in the main stem Klamath River upstream from major tributaries and in the Shasta River near the confluence with the Klamath River.

Fish Handling and Tagging

The mean fork length (FL mm) of hatchery and wild coho salmon tagged during the study period was 134 mm (SD = 11.6) and 147 mm (SD = 12.1), respectively. The mean weight of hatchery and wild coho salmon tagged was 25.3 g (SD = 7.21) and 33.7 g (SD = 6.63), respectively. Wild fish tagged in 2006 were significantly larger in terms of FL and weight compared to hatchery fish ($t_{0.05(2), 416} = 12.85, P < 0.001$), and ($t_{0.05(2), 416} = 10.6, P < 0.001$), respectively. The mean fork length (FL mm) of all wild coho captured at the CDFG rotary screw trap on the Shasta River was 145.5 mm (SD = 17.32). The subsample of wild fish we tagged were not significantly different in terms of FL compared to all wild coho captured emigrating from the Shasta River in 2006 ($t_{0.05(2), 521} = -0.38, P = 0.704$). The weight of radio transmitter (0.43 g in air) implanted in fish during 2006 represented an average of 1.63% of fish body weight (range = 0.66 to 3.63).

Release groups

We surgically implanted transmitters in a total of 390 juvenile coho salmon (213 hatchery; 177 wild) beginning 4 April and ending 24 May 2006. Because flow releases from IGD during the spring months are not predictable, and because obtaining large numbers of wild fish on demand was highly unlikely, we attempted to tag small replicate release groups (17 hatchery and wild fish) twice per week over a six week period coinciding with the peak downstream migration of wild fish from the Shasta River (Figure 13). Peak downstream migration timing of wild coho salmon from the Shasta River was delineated using CDFG trap data collected during the 2002-2005 period (Figure 14). This approach was developed to increase the likelihood of measuring juvenile coho salmon movement and survival in response to unpredictable changes in flows, and to allow comparison of survival estimates among hatchery and wild fish exposed to similar environmental conditions. The lack of wild fish from 5 April to 21 April 2006 caused us to extend tagging to an eight week period (Figure 13). We attempted to maintain equality in the number of wild and hatchery fish released at the test and control sites by dividing the number of fish allocated or captured on a given day into two equal groups (Table 3). When odd numbers of fish were collected, the one extra fish was released at the test site.

In addition to monitoring the river with fixed detection sites, mobile tracking began on 1 May 2006 to monitor movement between fixed sites. This mobile tracking start date was chosen because the expected tag life (45 d) of tags released on 4 April were nearing expiration and a final location of each tag was desired. The mobile tracking effort included the use of both vehicle-mounted and boat-mounted antennas, with the boat-mounted providing more precise tracking as the river flows decreased.

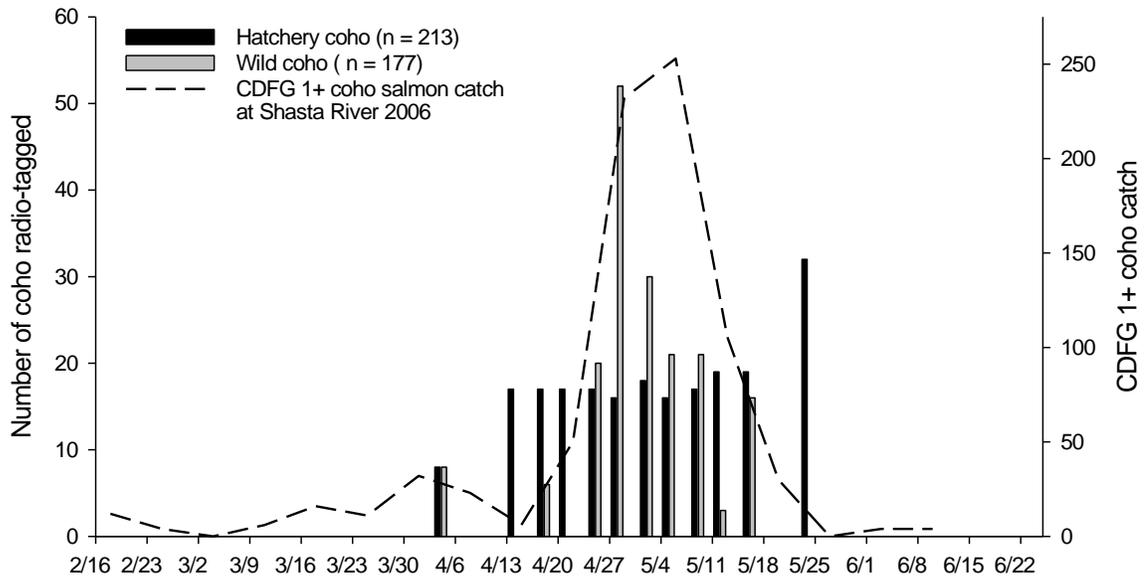


Figure 13. Number of wild and hatchery coho salmon radio-tagged, and number of 1+ coho salmon captured at the California Department of Fish and Game (CDFG) Shasta River rotary screw trap during the 2006 study period.

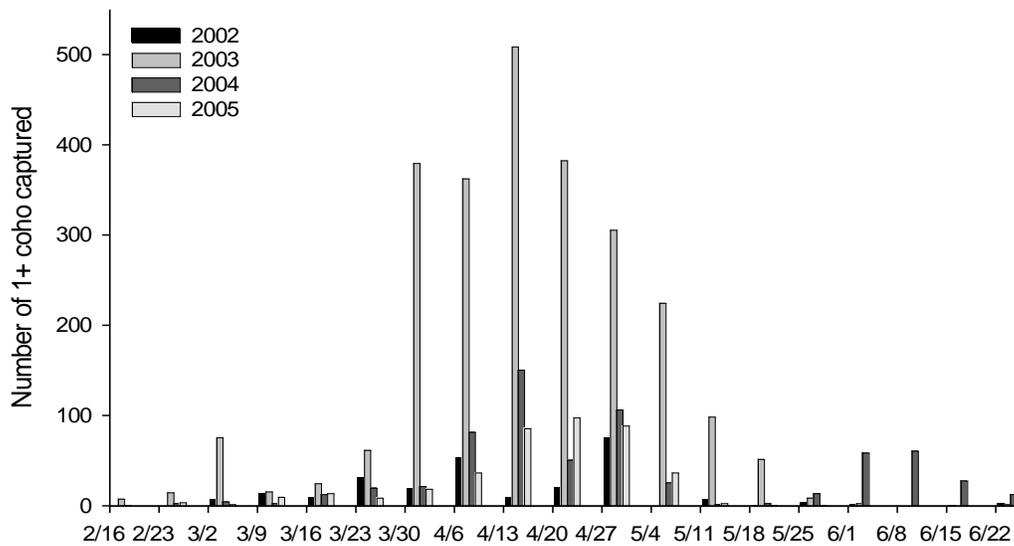


Figure 14. Weekly number of 1+ wild coho salmon captured at the California Department of Fish and Game (CDFG) rotary screw trap located near the mouth of the Shasta River (2002–2005). Data source: CDFG, (2002-2005).

Table 3. Date and number of radio-tagged wild (Shasta River), hatchery (IGH), and euthanized hatchery coho salmon released at test and control locations during the spring of 2006.

Date	Live				Euthanized	
	Wild		Hatchery		Hatchery	
	Test	Control	Test	Control	Test	Control
4 April	8	0	8	0	2	0
14 April	†	†	9	8	0	0
18 April	3 †	3 †	9	8	2	2
21 April	†	†	9	8	0	0
25 April	10	10	9	8	2	2
28 April	26	26	8	8	0	0
2 May	15	15	9	9	3	1
5 May	11	10	8	8	0	0
9 May	11	10	9	8	3	3
12 May	2 †	1 †	10	9	0	0
16 May	8	8	10	9	2	2
24 May	†	†	16	16	2	2
Totals	94	83	114	99	16	12

† Indicates dates where we were unable to implant the intended number of transmitters in wild coho salmon because insufficient numbers were collected.

Measures of Smoltification and Disease

Gill ATPase of Tagged fish

The ATPase activities of wild fish were statistically greater than those of hatchery fish, but little difference was apparent over time (Figure 15). The mean ATPase activity levels of fish from each tagging session ranged from 2-7 $\mu\text{mol P}_i \cdot \text{mg protein}^{-1} \cdot \text{h}^{-1}$ throughout the season. The mean ATPase activities of wild fish increased slightly over time after declining from the season high on the first sampling date (3 April), and ATPase activities were statistically different among dates (ANOVA, $F = 2.27$, $P = 0.0208$). The ATPase activities of hatchery fish were greatest on 24 April, and showed no significant change over time (ANOVA, $F = 1.22$, $P = 0.2692$). The mean ATPase activity of wild

fish (pooling dates; mean = 4.2) was statistically greater than the mean for hatchery fish (mean = 3.3; ANOVA, $F = 10.63$, $P = 0.0013$).

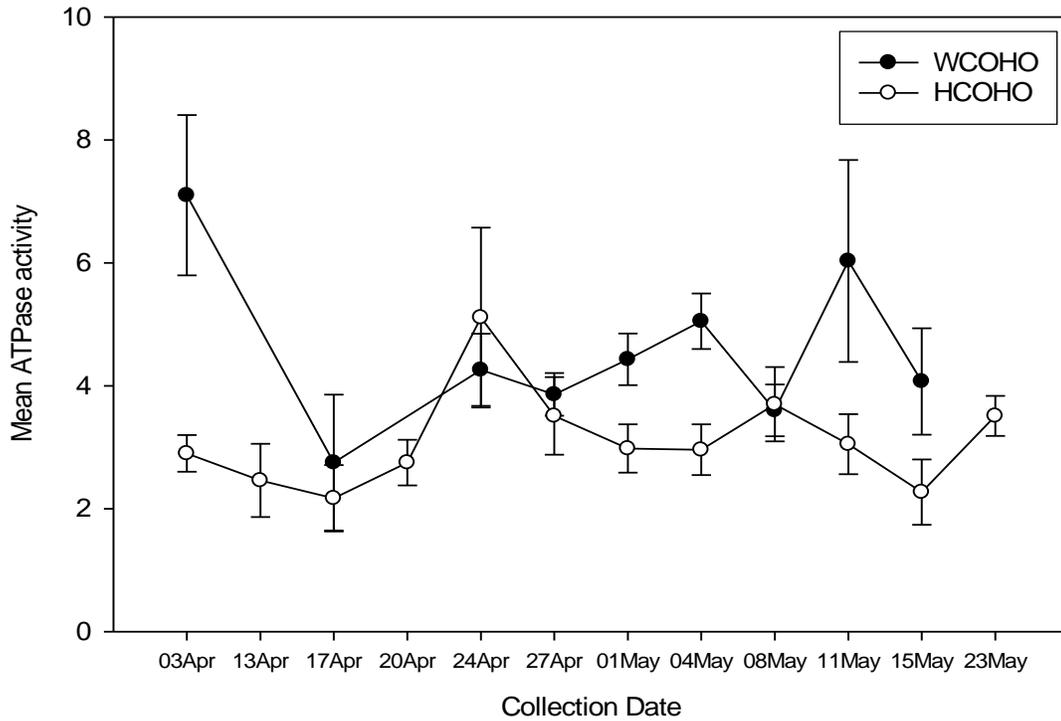


Figure 15. Mean gill ATPase activity levels of radio-tagged juvenile coho salmon during the spring of 2006. Wild coho salmon (filled symbols) were not available on all collection dates.

Gill ATPase of Untagged fish

The gill ATPase activity levels of the hatchery fish exposed to in-river conditions did not increase throughout the experiment as we would have expected, and were similar throughout the two trials (Figure 16). The general trend was a decrease in activity level from the start of each trial to the end of each trial. During the first trial we saw increasing activity levels in the first couple sample days, but the levels generally decreased during the rest of the sample days. The trend was similar in the second trial with initial activities levels increasing then trailing off during the remaining sample days (the day 21 sample was not collected due to poor fish health and mortalities). We attempted to capture a wide range of environmental indices (i.e., water temperature and photoperiod) by conducting

two trials that spanned from 19 April to 30 May, but the water temperature did not increase throughout that span. Water temperatures ranged from 10°C to 16°C during the first trial and hovered around 17°C for the duration of the second trial.

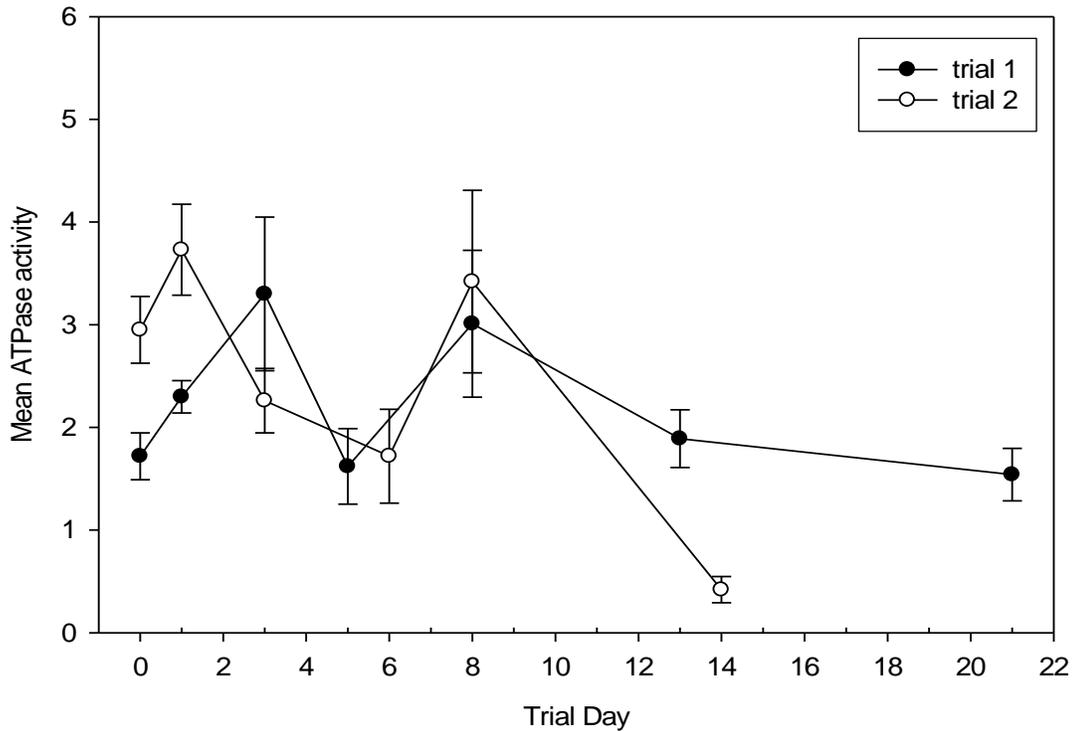


Figure 16. Mean gill ATPase activity of in-river exposure trials. Trial 1 (filled symbols) was conducted from 19 April to 10 May, and trial 2 (open symbols) was from 16 May to 30 May 2006.

There was a similar trend in ATPase activities in each trial characterized by two peaks prior to a general decrease to the end of each trial. The first peak occurred on day 4 in trial 1 and day 1 in trial 2, perhaps reflecting temperature or photoperiod differences between the trial periods. The second peak occurred on day 8 during both trials.

Bacterial Kidney Disease

The prevalence and severity of Bacterial Kidney Disease in the fish tested was low, but varied by analytical method. The qualitative nested PCR indicated 9 of the 65 fish (13.8%) tested positive for *R. salmoninarum*, the causative agent of the disease. Results

from the quantitative qPCR method indicated 13 of the 65 fish tested positive (20.0%), with all but one showing a low infection level (<1,000 bacteria in total extraction). The single fish that showed a different level of infection (3,125 bacteria in total extraction) was considered a medium infection level (Diane Elliott, U.S. Geological Survey, personal communication). Results are shown in Appendix 2.

Migration Analyses

Analyses of the migration behavior of hatchery and wild fish were based on data from dates on which reasonable numbers of each were released. These dates ranged from 25 April through 16 May 2006 and comprised 120 hatchery fish and 162 wild fish (Figure 17). These included releases of 57 hatchery control, 63 hatchery treatment, 79 wild control, and 83 wild treatment fish.

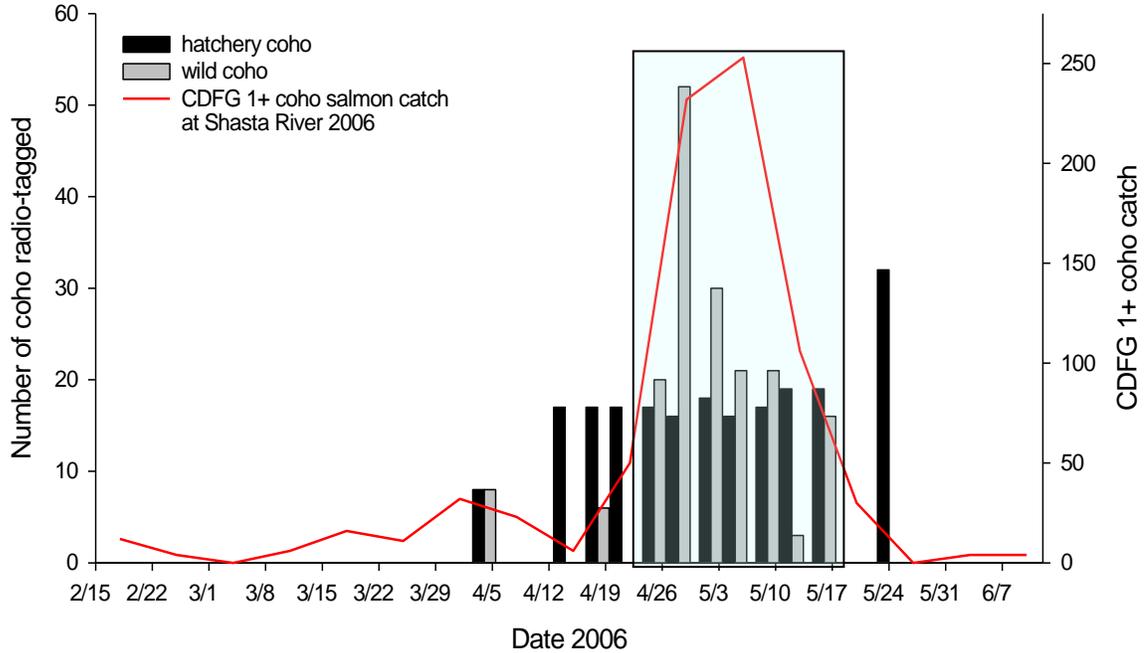


Figure 17. Number of wild and hatchery coho salmon radio-tagged in 2006, and those used for analysis (shaded region). Release dates ranged from 25 April through 16 May 2006 and comprised 120 hatchery fish and 162 wild fish.

The migrations of the two experimental groups were similar in all reaches, but differences among hatchery and wild fish existed throughout the study area. Travel times within the various reaches did not differ significantly between test and control groups of hatchery or wild fish within any of the five flow reaches (stratified comparisons of group controlling for origin, $P_s \geq 0.10$). However, migratory behavior of hatchery and wild fish (origin controlling for group) differed significantly in the first and second reaches, but not thereafter (reach 1 Wilcoxon Rank Sum Test $\chi^2 = 67.33$, $df = 1$, $P < 0.0001$; reach 2 $\chi^2 = 11.08$, $df = 1$, $P = 0.0009$).

The differences in migration of hatchery and wild fish were largely due to the long residence time of hatchery fish relative to wild fish in the first reach. The difference in passage timing that occurred in the first reach persisted throughout the study area and was still evident as fish passed at the last detection at Blake's Riffle (Figure 18). The time between release and migration past the Scott River diminished as the study period progressed and was more pronounced in hatchery fish than in wild fish (Table 4; Figure 19). As indicated in Figure 19, river discharge decreased and water temperature increased as travel times through the first reach decreased over time. Travel times of hatchery and wild fish through the lower three reaches were not significantly different, indicating that once hatchery fish initiated their downstream migration they traveled at rates similar to that of wild fish (Figure 20).

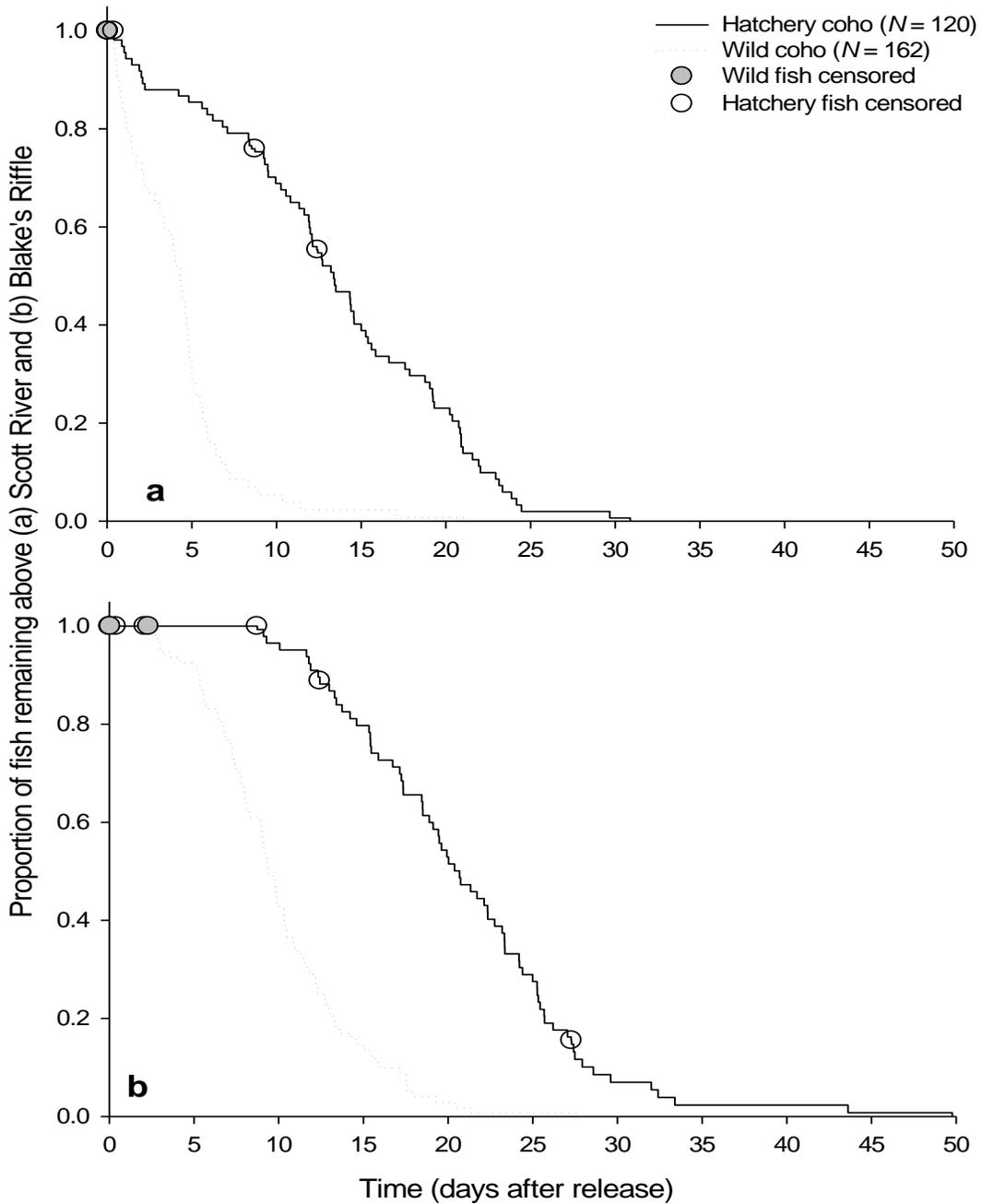


Figure 18. Kaplan-Meier curves describing travel times of radio-tagged hatchery and wild coho salmon following release to a) Scott River (rkm 234) and b) Blake's Riffle (rkm 13) detection sites during the spring of 2006. Open circles represent censored individuals.

Table 4. Median days (and range) radio-tagged coho salmon spent in each reach, by release date. Numbers below each reach designation are reach length. Sample sizes of wild coho ranged from 1 to 15 per row, with an average of 6.6. Sample sizes of hatchery coho ranged from 2 to 27 per row, with an average of 10. Sample size of one is denoted by na. Highlighted rows indicate release dates not used in migration analyses.

Release Date	Reach 1 (54 km)	Reach 2 (56 km)	Reach 3 (71 km)	Reach 4 (38 km)	Reach 5 (36 km)	Reach 5a (20 km)
-----Wild origin-----						
4/04/06	10.4 (5.0 - 29.3)	4.8 (1.8 - 8.5)	1.0 (0.7 - 4.7)	0.4 (0.2 - 1.4)	0.4 (0.2 - 5.5)	0.3 (0.1 - 1.5)
4/18/06	10.6 (5.4 - 18.9)	1.7 (0.5 - 4.1)	1.3 (1.2 - 1.7)	0.4 (0.2 - 0.7)	0.6 (0.5 - 3.1)	0.3 (0.1 - 0.8)
4/25/06	4.0 (1.9 - 10.7)	1.4 (0.4 - 4.9)	1.0 (0.4 - 4.4)	0.2 (0.2 - 0.6)	1.1 (0.2 - 1.2)	0.5 (0.1 - 0.7)
4/28/06	4.7 (0.8 - 21.3)	1.0 (0.4 - 3.9)	2.6 (0.8 - 6.6)	0.6 (0.2 - 1.0)	1.0 (0.3 - 6.8)	0.2 (0.1 - 2.7)
5/02/06	2.9 (0.8 - 6.8)	1.0 (0.3 - 2.5)	1.5 (0.7 - 8.9)	0.3 (0.2 - 1.3)	0.3 (0.2 - 1.6)	0.2 (0.1 - 0.6)
5/05/06	2.7 (0.4 - 10.2)	0.8 (0.7 - 0.9)	1.4 (0.9 - 2.7)	0.5 (0.3 - 1.6)	0.9 (0.3 - 2.0)	0.3 (0.1 - 2.9)
5/09/06	0.6 (0.3 - 2.1)	0.9 (0.4 - 6.0)	1.4 (0.6 - 3.6)	0.5 (0.2 - 1.1)	1.0 (0.2 - 8.2)	0.2 (0.1 - 1.1)
5/12/06	0.3 (0.3-0.3)	0.6 (0.5 - 0.7)	0.4 (na)	0.4 (na)	0.3 (0.2 - 0.5)	0.5 (0.2 - 0.8)
5/16/06	3.9 (1.0 - 4.3)	4.6 (na)	1.6 (0.8-7.4)	0.8 (0.2 - 2.0)	0.4 (0.2 - 0.6)	0.7 (0.7 - 0.9)
Overall	3.9 (0.3 - 29.3)	1.0 (0.3 - 8.5)	1.4 (0.4 - 8.9)	0.5 (0.2 - 2.0)	0.7 (0.2 - 8.2)	0.2 (0.1 - 2.9)
-----Hatchery origin-----						
4/04/06	7.2 (0.3 - 14.0)	1.1 (0.7 - 1.6)	1.3 (0.5 - 3.5)	0.5 (0.2 - 1.0)	2.5 (0.2 - 4.9)	0.4 (0.1 - 0.6)
4/14/06	5.5 (0.5 - 29.7)	0.7 (0.4 - 1.0)	0.8 (0.4 - 7.0)	0.2 (0.2 - 2.4)	0.6 (0.2 - 2.2)	0.6 (0.1 - 1.4)
4/18/06	21.3 (0.6 - 32.5)	1.3 (0.3 - 3.0)	1.2 (0.7 - 3.7)	0.3 (0.2 - 3.8)	1.1 (0.7 - 10.1)	0.4 (0.1 - 2.0)
4/21/06	17.0 (0.4 - 28.9)	1.2 (0.3 - 4.5)	1.2 (0.7 - 1.8)	0.3 (0.2 - 2.0)	0.7 (0.2 - 2.3)	0.4 (0.1 - 0.9)
4/25/06	19.6 (0.4 - 30.9)	1.1 (0.3 - 24.7)	0.6 (0.3 - 1.7)	0.2 (0.2 - 0.6)	1.1 (0.2 - 6.3)	0.3 (0.1 - 1.1)
4/28/06	14.7 (0.4 - 23.3)	1.1 (0.5 - 5.0)	1.9 (0.4 - 5.8)	0.4 (0.2 - 2.0)	0.4 (0.2 - 2.2)	0.3 (0.1 - 1.5)
5/02/06	3.8 (0.6 - 29.7)	0.7 (0.3 - 6.4)	1.2 (0.4 - 3.5)	0.6 (0.2 - 1.1)	0.6 (0.2 - 2.4)	0.1 (0.1 - 2.2)
5/05/06	12.6 (0.4 - 14.6)	2.8 (0.3 - 8.3)	2.0 (0.4 - 9.8)	0.5 (0.2 - 2.9)	0.3 (0.2 - 5.2)	0.2 (0.1 - 1.0)
5/09/06	5.4 (1.0 - 8.4)	3.2 (0.3 - 16.9)	2.0 (0.5 - 5.9)	0.4 (0.2 - 1.9)	1.0 (0.8 - 5.2)	0.9 (0.1 - 2.0)
5/12/06	6.2 (0.4 - 17.9)	2.7 (0.5 - 20.9)	1.3 (0.9 - 7.4)	0.9 (0.2 - 5.1)	0.7 (0.2 - 2.1)	0.3 (0.1 - 2.0)
5/16/06	1.7 (0.4 - 10.1)	4.2 (0.3 - 11.0)	1.3 (0.4 - 8.2)	1.1 (0.2 - 6.1)	0.9 (0.2 - 2.0)	0.3 (0.1 - 1.1)
5/24/06	6.5 (0.9 - 11.0)	3.0 (0.4 - 11.9)	1.6 (0.6 - 10.6)	0.5 (0.2 - 5.1)	0.9 (0.2 - 8.7)	0.2 (0.1 - 7.8)
Overall	6.5 (0.3 - 32.5)	1.6 (0.3 - 24.7)	1.3 (0.3 - 10.6)	0.4 (0.2 - 6.1)	0.8 (0.2 - 10.1)	0.3 (0.1 - 7.8)

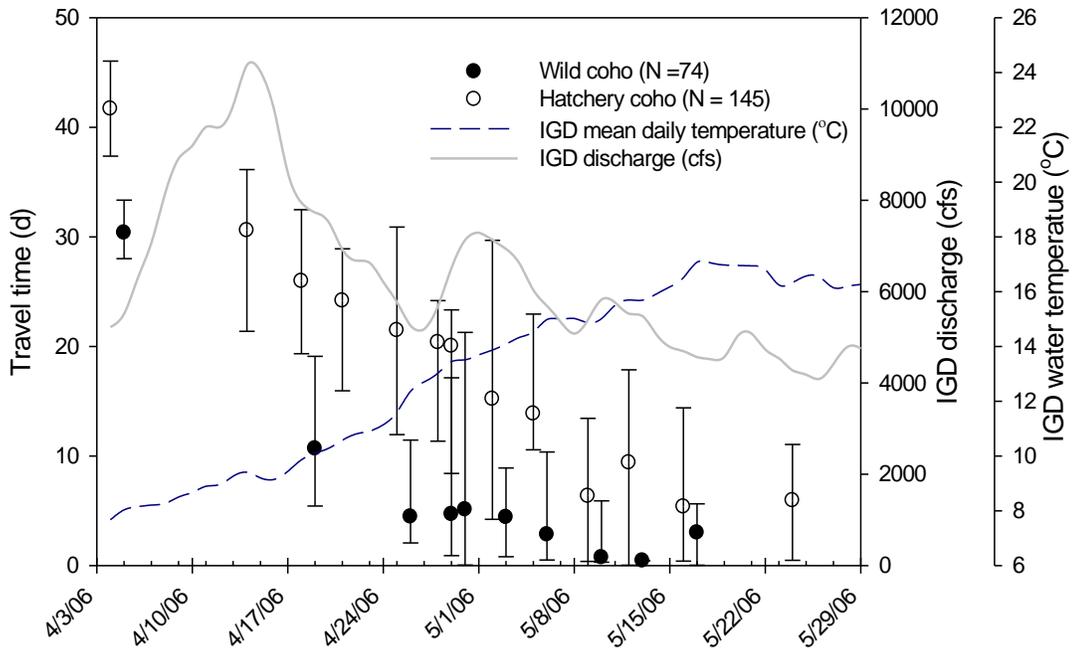


Figure 19. Median travel times of radio-tagged hatchery and wild coho salmon from release to Scott River (rkm 234) during the spring of 2006 relative to mean daily discharge from Iron Gate Dam and mean daily water temperature within the reach. Circles represent median travel times of test and control release groups released on common dates, error bars represent the range. Release dates of wild fish were offset by +1d to prevent data from overlapping in the plot.

Regression analyses were performed to examine potential covariates of travel times in each of the uppermost three reaches. We focused only on these reaches because: a) there were no differences in survival distribution functions between hatchery and wild fish in reaches after the third (Indian Creek to Salmon River), and b) river discharge was not a significant predictor variable in either of the second or third reaches, and thus analyses of subsequent reaches seemed unwarranted.

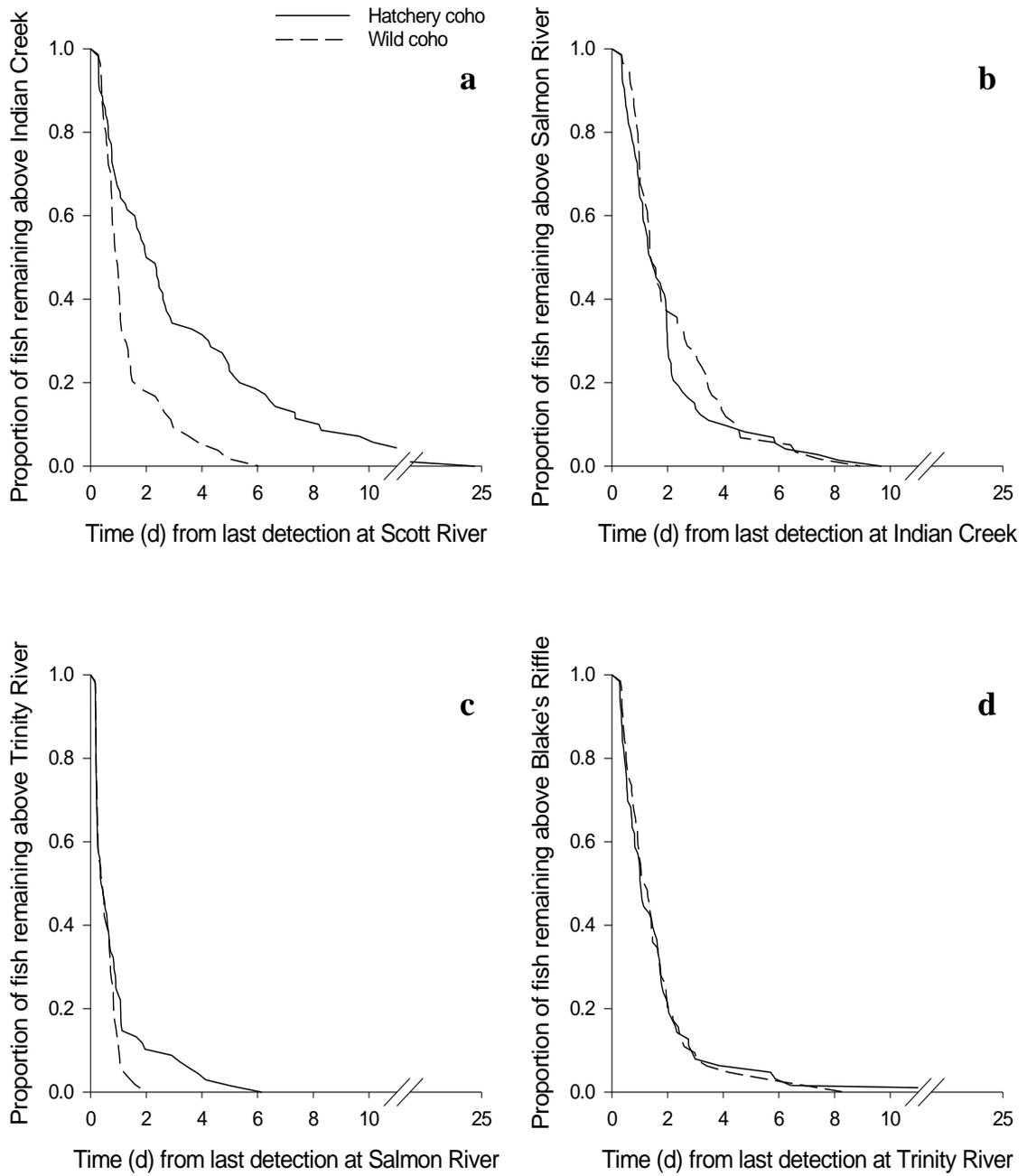


Figure 20. Kaplan-Meier curves of travel times of radio-tagged hatchery and wild coho salmon through intermediate flow reaches a) Scott River to Indian Creek, b) Indian Creek to Salmon River, c) Salmon River to Trinity River, and d) Trinity River to Blake's Riffle during the spring of 2006. Data are from 162 wild fish and 120 hatchery fish released from 25 April through 16 May 2006.

Models of covariates in Reach 1 (release to Scott River)

Assessment of model assumptions indicated few violations. Martingale residuals and plots of slope parameter estimates over discrete values of river discharge in the first reach

indicated a slight curvilinear trend. Linearity was improved by using the natural logarithm of river discharge, so this form was used in all analyses. Fish weight violated the proportional hazards assumption in Reach 1 (interaction term $P = 0.0185$, $df = 1$), but using the natural log of weight resulted in some improvement ($P = 0.0546$, $df = 1$), so this form was used in analyses. No other variables violated this assumption or that of linearity. The variables serial date of release, log of discharge, and water temperature were significantly correlated (absolute value of correlation coefficients, $|r|, \geq 0.75$, $P_s < 0.0001$; Table 5), so regression models were developed with each variable separately.

The final regression model using discharge in the first reach included origin, log discharge, log weight, and the interaction between origin and log discharge (Table 6). The model expresses results in terms of the hazard, or rate, of passage at the measurement site (Scott River), but we will express their effects here in general terms of the travel time for consistency with earlier sections. The presence of the significant interaction between origin and log of discharge affects the interpretation of the effects of log discharge on travel times of hatchery (origin = 0) vs. wild (origin = 1) fish. The model describes longer travel times of hatchery fish than wild fish, an increase in travel time as discharge increases, and a much smaller effect of discharge on the travel times of wild fish than hatchery fish. For hatchery fish, the model simplifies to one of the effects of log discharge and log weight. Here the factors affected by origin are not used because the origin variable for hatchery fish is zero; this removes the origin and origin-log discharge interaction terms from the model of hatchery fish. The origin variable is one for wild fish, so the origin term and the origin-log discharge interaction term are used here to 1) reduce travel time and 2) reduce the effects of discharge from those predicted for hatchery fish.

This model predicts that the travel time of hatchery fish increases with discharge to a greater extent than that of wild fish. The top plate in Figure 21 illustrates predicted model output at discharges of 4,770 and 6,002 cfs, which are the 25th and 75th percentiles of discharge values in the data analyzed. The model predicted that the median travel times of wild fish would change from 4.2 to 4.4 days (a 5% increase) and those of

Table 5. Pearson product-moment correlation coefficients and *P*-values (in italics) from t-tests of their association. Serdate is the serial date of release, LogQ is the natural log of river discharge in each reach, and logwt is the natural log of fish weight at the time of tagging. Event is the time to travel through each reach.

----- Reach 1 -----						
	Serdate	LogQ	Temp	Logwt	ATPase	Event
Serdate	1	-0.7971 <i><.0001</i>	0.8898 <i><.0001</i>	-0.2047 <i><.0001</i>	-0.1603 <i><.0001</i>	0.1467 <i><.0001</i>
LogQ		1	-0.7544 <i><.0001</i>	0.1510 <i><.0001</i>	0.1236 <i><.0001</i>	-0.1233 <i><.0001</i>
Temp			1	-0.2153 <i><.0001</i>	-0.1415 <i><.0001</i>	0.1181 <i><.0001</i>
Logwt				1	-0.0608 <i>0.0166</i>	-0.5330 <i><.0001</i>
ATPase					1	0.0813 <i>0.0013</i>
----- Reach 2 -----						
	Serdate	LogQ	Temp	Logwt	ATPase	Event
Serdate	1	-0.2976 <i><.0001</i>	0.0842 <i>0.0700</i>	0.2436 <i><.0001</i>	-0.3020 <i><.0001</i>	0.1027 <i>0.0269</i>
LogQ		1	-0.6638 <i><.0001</i>	0.2470 <i><.0001</i>	0.2181 <i><.0001</i>	-0.6389 <i><.0001</i>
Temp			1	-0.2599 <i><.0001</i>	-0.1108 <i>0.0169</i>	0.5481 <i><.0001</i>
Logwt				1	-0.1751 <i>0.0001</i>	-0.1241 <i>0.0074</i>
ATPase					1	-0.2030 <i><.0001</i>
----- Reach 3 -----						
	Serdate	LogQ	Temp	Logwt	ATPase	Event
Serdate	1	-0.5164 <i><.0001</i>	0.3506 <i><.0001</i>	-0.0519 <i>0.2958</i>	-0.1830 <i>0.0002</i>	0.1379 <i>0.0053</i>
LogQ			-0.4696 <i><.0001</i>	0.0348 <i>0.4836</i>	0.1817 <i>0.0002</i>	-0.1490 <i>0.0025</i>
Temp			1	-0.1270 <i>0.0102</i>	-0.1865 <i>0.0002</i>	-0.0613 <i>0.2169</i>
Logwt				1	0.0846 <i>0.0880</i>	0.0448 <i>0.3670</i>
ATPase					1	-0.0681 <i>0.1698</i>

Table 6. Output from the final Cox regression models from Reaches 1, 2, and 3. The Standard Error Ratio is a measure of the reduction in error associated with the use of the Robust sandwich estimates ($< 1 =$ reduced error). Variable denoted “a” is involved in a significant interaction and the hazard ratio must be computed with parameter estimates of both the main effect and the interaction. $df = 1$ for all rows.

Variable	Parameter Estimate	Standard Error	Standard Error Ratio	ChiSquare	Pr > Chisq	Hazard Ratio	95% Hazard Ratio Confidence Limits	
-----Reach 1 with Discharge-----								
Origin	-50.737	12.466	0.971	16.565	<.0001	a	a	a
LogQ	-6.594	1.449	1.174	20.707	<.0001	a	a	a
Logwt	0.560	0.264	0.816	4.507	0.0338	1.751	1.044	2.937
Origin_Q	6.116	1.453	0.967	17.730	<.0001	a	a	a
-----Reach 1 with Temperature-----								
Origin	9.213	2.568	0.853	12.869	0.0003	a	a	a
Temperature	0.786	0.160	1.097	23.965	<.0001	a	a	a
Logwt	0.787	0.246	0.766	10.215	0.0014	2.197	1.356	3.561
Origin_Temp	-0.481	0.166	0.866	8.375	0.0038	0.618	0.446	0.856
-----Reach 1 with Serial Release Date-----								
Origin	1.841	0.308	1.410	35.837	<.0001	6.302	3.449	11.513
Release Date	0.102	0.015	1.098	44.347	<.0001	1.108	1.075	1.141
Logwt	0.927	0.337	1.054	7.560	0.0060	2.527	1.305	4.895
-----Reach 2-----								
Origin	0.812	0.222	1.105	13.454	0.0002	2.254	1.46	3.479
ATPase	0.058	0.032	0.779	3.321	0.0684	1.06	0.996	1.129
-----Reach 3-----								
Logwt	- 0.487	0.257	0.766	3.380	0.0585	0.615	0.371	1.018

hatchery fish would change from 8.5 to 23.0 d (a 170% increase) at river discharges of 4,770 cfs and 6,002 cfs, respectively. Results of the Goodness-of-Fit test indicate the model fit the data (Likelihood Ratio Test statistic = 15.1, $df = 9$, $P = 0.0889$). The AIC values ranged from 1,100 for the full model to 1,092 for the final model, were reduced by a value of about 2 as each variable was removed, and indicated the models with fewer parameters were more parsimonious. The predicted shorter travel times at greater discharges is supported by the pattern of travel time and discharge observed in 2006.

The final model using temperatures in the first reach included origin, temperature, log weight, and the interaction of origin and temperature (Table 6). The sign of the

parameter estimates of origin, temperature, and log weight were positive and the interaction term of origin and temperature was negative. Thus, the model predicts that travel time of wild fish is faster than hatchery fish, and is faster at higher temperatures and for heavier fish. The negative sign for the interaction term indicates the effect of water temperature is greater for hatchery fish than for wild fish. The predicted relation between travel time and temperature for hatchery and wild fish is shown in the middle plate of Figure 21. The model predicted the median travel times at 14°C and 16°C would be 4.8 d and 2.3 d for wild fish (a 52% reduction) and 24.4 d and 9.2 d for hatchery fish (a 62% reduction). Results of the Goodness-of-Fit test indicated the model fit the data (Likelihood Ratio Test statistic = 15.2, $df = 9$, $P = 0.0849$). The AIC values ranged from 1,098 for the full model to 1,090 for the final model, were reduced by a value of about 2 as each variable was removed, and indicated the models with fewer parameters were more parsimonious.

The final model using release date included origin, serial date of release, and log weight (Table 6). No significant interaction terms were present. The model indicates the travel times were reduced as release date increased and weight increased and that wild fish had shorter travel times than hatchery fish. The model predicts median travel times on 28 April and 5 May would be 5.9 days and 4.1 days for wild fish (a 30% reduction) and 17.6 days and 12.4 days for hatchery fish (a 29% reduction; dates represent 25th and 75th percentiles of the data; Figure 20, lower plate). Results of the Goodness-of-Fit test indicate the model fit the data (Likelihood Ratio Test statistic = 15.4, $df = 9$, $P = 0.0785$). The AIC values ranged from 1,085 for the full model to 1,075 for the final model, were reduced by a value of about 2 as each variable was removed, and indicated the models with fewer parameters were more parsimonious.

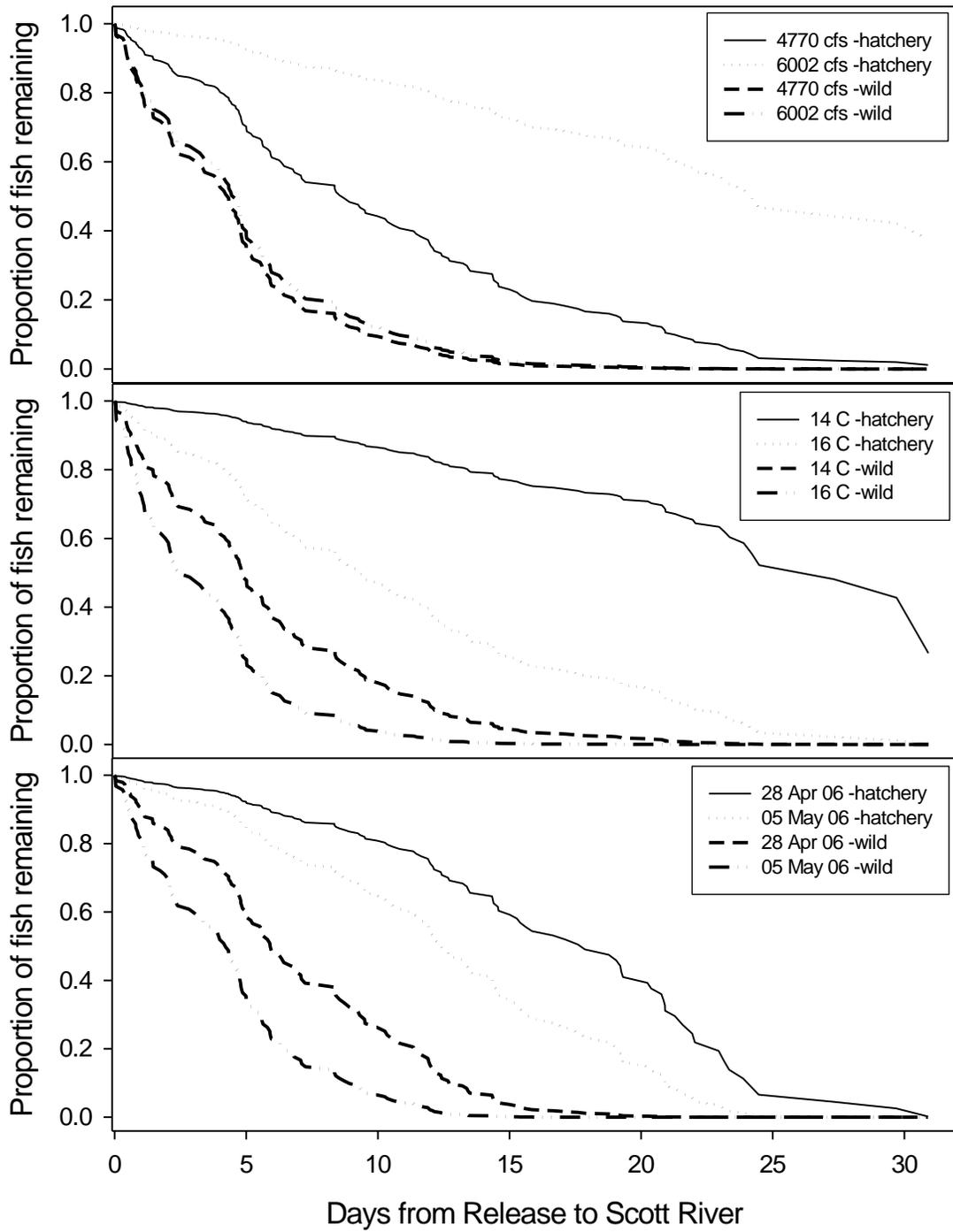


Figure 21. Model predictions of the effects of discharge, water temperature, and release date on event times in Reach 1. Plots are at the 25th and 75th percentiles of each variable.

Models of covariates in Reach 2 (Scott River to Indian Creek)

In data from Reach 2 several variables failed to meet model assumptions and were not used in analyses. Serial date of release and water temperature violated the proportional hazards assumption, as indicated by significant interaction with time ($P_s < 0.05$). All variables examined appeared to meet the linearity assumption. Thus, unlike Reach 1 analyses in which models were examined with discharge, serial release date, and water temperature separately, only models with discharge and other variables (without serial release date and water temperature) were examined in Reach 2.

The final regression model from Reach 2 included origin and ATPase (Table 6). The origin variable was highly significant ($P = 0.0002$) and the ATPase variable was marginally significant ($P = 0.0684$). The parameter estimates of both variables were positive, indicating the travel times of wild fish were shorter than hatchery fish and travel times were shorter for fish with higher ATPase activities (also characteristic of the difference between hatchery and wild fish). The log of discharge was not included in the final model, as it was clearly not significant ($P = 0.8600$). The model predicted the median travel time of wild fish with their median ATPase activity ($4.2 \mu\text{mol P}_i \cdot \text{mg protein}^{-1} \cdot \text{h}^{-1}$) would be 0.9 d and that of hatchery fish at their median ATPase activity ($2.9 \mu\text{mol P}_i \cdot \text{mg protein}^{-1} \cdot \text{h}^{-1}$) would be 2.0 d (2.2 times longer than the wild fish; Figure 22). The use of the Robust Sandwich Variance estimates was not conclusively advantageous in this analysis. Their use increased the variance of the origin parameter by 10% and decreased the variance of the ATPase parameter by 20%. The ATPase parameter was not a significant model contributor when the Robust sandwich variance estimates were not used ($P = 0.1557$), but the significance of the origin parameter changed little with or without the adjustment ($P < 0.0001$ vs. $P = 0.0002$). It should be noted that the Robust Sandwich Variance method affects the variance of the parameter estimates, but not the parameter estimates themselves, hence the meaning of the model changes little with or without this adjustment. Results of the Goodness-of-Fit test indicate the model fit the data (Likelihood Ratio Test statistic = 6.4, $df = 9$, $P = 0.6950$). The AIC values ranged from 948 for the full model to 938 for the final model, were

reduced by a value of about 2 as each variable was removed, and indicated the models with fewer parameters were more parsimonious.

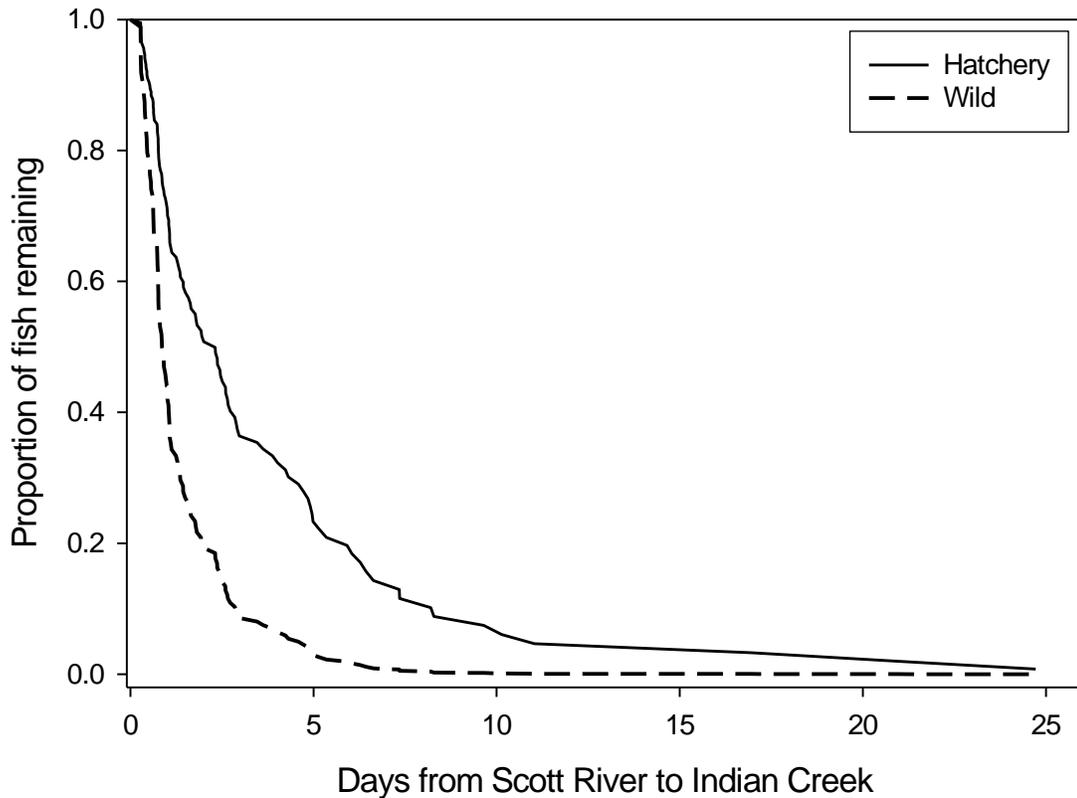


Figure 22. Model predictions of the effects of fish origin on travel times in Reach 2. Plots are at the median ATPase activities of hatchery fish ($2.9 \mu\text{mol P}_i \cdot \text{mg protein}^{-1} \cdot \text{h}^{-1}$) and wild fish ($4.2 \mu\text{mol P}_i \cdot \text{mg protein}^{-1} \cdot \text{h}^{-1}$).

Models of covariates in Reach 3 (Indian Creek to Salmon River)

No variables were omitted from analyses of Reach 3 based on model assumptions or correlations among them. All variables met model assumptions of linearity and proportional hazards. As in the previous reach analyses, serial date of release, discharge, and water temperature were significantly correlated ($P < 0.05$), but in Reach 3 the correlation coefficients were moderate ($|r|$ less than about 0.5), so these variables were used together in regression models.

The log of weight was the only significant contributor to the travel time through Reach 3 ($P = 0.0585$; Table 6). The full model included seven main effects and seven interaction terms. The main effects were group, origin, log of weight, log of discharge, ATPase, water temperature, and serial date of release. The interaction terms were selected combinations of the main effects. As the model was reduced, only log weight remained as a moderately significant predictor of the time to the event ($P = 0.0585$). The sign of the slope coefficient was negative, indicating travel times were shorter for lighter fish. This result is unlike the relation in Reach 1; however, results of the Goodness-of-Fit test indicate the model of Reach 3 was a poor fit to the data (Likelihood Ratio Test statistic = 18.3, $df = 9$, $P = 0.0314$). The AIC values ranged from 1,049 for the full model to 1,032 for the final model, were reduced by a value of about 2 as each variable was removed, and indicated the models with fewer parameters were more parsimonious.

Survival Analyses

Survival analyses were conducted using: 1) hatchery and wild fish released on common dates with reasonable numbers released and 2) hatchery fish from all release dates. The data used in the hatchery and wild comparisons were released from 25 April through 16 May 2006 and comprised 120 hatchery fish and 162 wild fish (as in migration analyses; Figure 17). These included releases of 57 hatchery control, 63 hatchery treatment, 79 wild control, and 83 wild treatment fish. Fish from all dates were pooled for survival and capture probability analyses, because the data were too sparse to support models with parameters for each release date. There were 43 unique encounter histories, with those of fish released and detected at all sites (1111111) and released and never detected (1000000) being the most prevalent in each of the four categories (hatchery control, hatchery treatment, wild control, wild treatment; Appendix 3). Analyses based on all hatchery fish releases included 114 treatment and 97 control fish released between 4 April and 24 May 2006. As in analyses of hatchery and wild fish, models allowing capture probabilities to vary among sites were chosen. There were 27 unique encounter histories, with those released and never detected and released and detected at all sites the most common (Appendix 4).

Capture Probabilities

The most parsimonious models of capture probabilities of the hatchery and wild analyses included additive effects of origin and site. The capture probabilities of wild fish were lower than hatchery fish at each site (Table 7). Capture probabilities of wild fish ranged from 0.466 to 0.864 among sites, and those of hatchery fish ranged from 0.835 to 0.974. The low probabilities were attributed to poor performance of some receivers and the faster migration of wild fish relative to hatchery fish in some reaches. Receiver adjustments were made on 15 May 2006, but most wild fish had left the study area by that date. The capture probabilities were generally highest at the Indian Creek site and lowest at the Scott River site. This model of capture probability was used in most models examined. Other models of capture probability were seldom used and were never part of models receiving high model weights.

Models in which capture probabilities could vary by site were about equally supported by the hatchery-only data as those that assumed a single capture probability for all sites and a model based on sites and group. Inasmuch as each model received similar support and choosing any one of them would have little bearing on the estimated survival, we chose to use the model allowing p to vary by site; this model is biologically reasonable and is consistent with the models based on hatchery and wild fish described earlier. In this model, capture probabilities ranged from 0.850 at the Scott River site to 0.965 at the Indian Creek site (Table 8).

Release of Euthanized Radio-Tagged Fish

Records from several euthanized fish were present in the raw data, but they were not considered valid records and were excluded. There were records from one fish each at the Shasta River, Scott River, and Blake's Riffle sites; the records from each fish were only present at a single site. Records at the Shasta and Scott sites were consistent with general noise and were excluded during the standardized data proofing process. The records of the single euthanized fish at Blake's Riffle were the only records from that fish

Table 7. Estimated capture probabilities, standard errors, and 95% confidence intervals of radio-tagged juvenile coho salmon at the first five detection sites in the Klamath River during spring, 2006. Data are from 162 wild fish and 120 hatchery fish released from 25 April through 16 May 2006.

Site #	Site Description	Capture Probability	Standard Error	95% Confidence Interval	
				Lower	Upper
----- Wild Origin -----					
1	Scott River (rkm 234)	0.466	0.050	0.371	0.563
2	Indian Creek (rkm 178)	0.864	0.037	0.773	0.922
3	Salmon River (rkm 107)	0.575	0.053	0.470	0.674
4	Trinity River (rkm 69)	0.710	0.050	0.605	0.797
5	Steelhead Lodge (rkm 33)	0.579	0.058	0.464	0.686
----- Hatchery Origin -----					
1	Scott River (rkm 234)	0.835	0.035	0.753	0.893
2	Indian Creek (rkm 178)	0.974	0.010	0.946	0.987
3	Salmon River (rkm 107)	0.887	0.028	0.820	0.931
4	Trinity River (rkm 69)	0.934	0.019	0.887	0.963
5	Steelhead Lodge (rkm 33)	0.888	0.029	0.818	0.934

Table 8. Estimated capture probabilities, standard errors, and 95% confidence intervals of 211 radio-tagged hatchery juvenile coho salmon released from 4 April through 24 May 2006. Results are based on pooling fish of treatment and control groups.

Site #	Site Description	Capture Probability	Standard Error	95% Confidence Interval	
				Lower	Upper
----- Hatchery Origin -----					
1	Scott River (rkm 234)	0.850	0.029	0.784	0.898
2	Indian Creek (rkm 178)	0.965	0.016	0.918	0.985
3	Salmon River (rkm 107)	0.886	0.027	0.822	0.929
4	Trinity River (rkm 69)	0.897	0.026	0.834	0.938
5	Steelhead Lodge (rkm 33)	0.920	0.024	0.858	0.956

(i.e., it was not heard at any of the six sites upstream), were near the noise criteria, and occurred after the detection equipment at the Salmon River was removed and the data collection period of study had effectively ended. Thus, the records from euthanized fish were logically excluded from the data and no evidence of violating assumption A7 was evident based on euthanized fish released.

During the mobile tracking effort euthanized fish were detected regularly, and downstream drifting was monitored to determine distance from the release site. Fifty percent (8 of 16) of dead fish released at IGH were later located via mobile-tracking. Dead fish released at this location drifted an average of 2.8 km (range 0.7 to 7.2 km). Daily mobile tracking began on 1 May, and no dead fish released at this site prior to that date were found. Of the 12 dead fish released at the control site (rkm 288), eight (66.7%) were later located during mobile tracking. Dead fish released at the control site drifted an average of 7.4 km (range 0.3 to 19.9 km).

Relative Survival from Iron Gate Hatchery to the Shasta River

Estimates of the treatment group survival relative to the control group survival were made using the paired-release design to estimate survival from IGH to the Shasta River without potential tagging and handling effects. Wild and hatchery origins were analyzed separately. Plots of deviance residuals (difference between the observed and expected frequencies of capture histories) indicated no patterns or large deviations from expected frequencies, and therefore indicated no obvious signs of model misspecification. The tests of model fit indicated moderate overdispersion, suggesting the variances would be underestimated. We corrected for this by applying a variance inflation factor median \hat{c} of 1.540 to analyses of wild fish and 1.459 to those of hatchery fish, adding 1 to the number of estimable parameters in each model to account for the use of \hat{c} , and using the quasi-likelihood adjusted AICc (QAICc), to rank models. This procedure inflates variances and slightly alters model-ranking results (Burnham and Anderson 1998). Estimates of survival were based on model-averaged results following the protocols of Burnham et al. (1987; Appendices 5 and 6)

The relative survival estimates indicate mortalities of treatment fish from release to the Shasta River were within the error of the estimates. Relative survival of wild coho salmon in this reach was 1.115 (95% CI 0.856-1.374), indicating control and treatment fish had similar survivals, despite traveling different distances (Table 9). Relative survival of hatchery coho salmon from release to the Shasta River was 0.994 (95% CI

0.790-1.198), indicating no detectable mortality of the treatment group in this reach, though the confidence intervals were wide. Estimates of relative survival of both wild and hatchery treatment and control groups in the next two reaches were 0.985 or greater, indicating similar mortality of both groups in the common reaches. Thus, no chronic mortality due to tagging and handling was observed and data from subsequent reaches were not examined.

Table 9. Estimated relative survivals, standard errors, and 95% confidence intervals of radio-tagged juvenile coho salmon in each of the first three study reaches in the Klamath River during spring, 2006. Data are from 162 wild fish and 120 hatchery fish released from 25 April through 16 May 2006. Results are based the ratio of treatment group survival divided by the control group survival within each reach. Treatment fish were released at Iron Gate Hatchery (IGH; rkm 309) and control fish were released at the confluence of the Klamath and Shasta rivers (rkm 288). As such, the first reach represents survival of the treatment group from Iron Gate Hatchery to the control release site. Both groups traveled the same distance through the remaining reaches.

Description	Reach Length (km)	Relative Survival	Standard Error	95% Confidence Interval	
				Lower	Upper
----- Wild Origin -----					
IGH to Shasta River	21	1.115	0.132	0.856	1.374
Scott River to Indian Creek	56	0.987	0.088	0.814	1.160
Indian Creek to Salmon River	71	1.000	0.058	0.886	1.113
----- Hatchery Origin -----					
IGH to Shasta River	21	0.994	0.104	0.790	1.198
Scott River to Indian Creek	56	0.985	0.065	0.858	1.111
Indian Creek to Salmon River	71	0.998	0.053	0.895	1.101

Survival through the Study Reaches

Hatchery vs. Wild

Survival through the study reaches was estimated using the single-release design. The most parameterized models fit the data reasonably well. Plots of deviance residuals indicated no patterns or large deviations from expected frequencies, and therefore indicated no obvious signs of model misspecification. The test of model fit indicated moderate overdispersion, suggesting the variances would be underestimated. We

corrected for this by applying a median c-hat value of 1.510 and following the steps described in the previous section.

There was no model clearly superior to all others in the set of seven models evaluated. Model weights (QAICc) were similar among the top four models (within about a factor of 5 of the top model), indicating they were all supported by the data (Table 10). The weight of the fifth model was 15 times less than the top model, indicating little support by the data, and those of the last two models were 10,000 times or less than the top model, indicating virtually no support.

Table 10. Model summary from analyses of apparent survival and capture probabilities to estimate reach survivals. Models are based on data from 162 wild fish and 120 hatchery fish released from 25 April through 16 May 2006. Model descriptions include factors allowed to vary within apparent survival (Phi) including reach, group (treatment or control), and origin (wild or hatchery). GroupAcute denotes a model factor for an acute group effect in the first reach only. Rankings are based on QAICc, a modification of Akaike Information Criterion for small samples and adjustments of extrabinomial variation. A '+' between factors indicates an additive effect and '*' denotes a multiplicative effect. A Reach+Origin model of capture probability (P) is common to all but the global model, which includes multiplicative effects of all factors for Phi and P. Num. Parm. denotes the number of estimable parameters in the model.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Parm.	QDeviance
Phi(Reach)	1102.6	0.0	0.45	1.00	12	158.3
Phi(GroupAcute+Reach)	1103.6	1.1	0.26	0.59	13	157.4
Phi(Reach+Origin)	1104.6	2.1	0.16	0.36	13	158.3
Phi(Reach+Origin+GroupAcute)	1105.7	3.1	0.09	0.21	14	157.4
Phi(Group*Origin+Reach)	1108.3	5.7	0.03	0.06	15	157.9
Phi(Origin*Group*Reach)	1122.2	19.6	0.00	0.00	27	146.8
global model	1137.9	35.3	0.00	0.00	40	134.7

The model with the largest weight allowed survival to vary by site only; the effect of site was moderate, with slope (beta) coefficients similar in size to their standard errors (SE), resulting in confidence intervals overlapping zero. The second ranked model allowed survival to vary by site and included an acute effect of group in the first reach only; the effect of the acute group effect was moderate (beta = -0.40, SE = 0.41). The third ranked model allowed survival to vary by site and origin, but the SE of the beta

coefficient for origin was much larger than the coefficient itself, indicating an unimportant effect ($\beta = 0.008$, $SE = 0.28$). The fourth model allowed survival to vary by site and origin with an acute effect of group in the first reach; in this model the beta of origin was important as in previous models, but the effect of acute group factor was moderate ($\beta = -0.40$, $SE = 0.41$). The last three models were not considered.

The data and models considered provide little support for differences in survival between experimental groups in the first reach, or between wild and hatchery fish. We therefore estimated the apparent survival within each reach, and subsequently over them all, using the output from the most supported model (the top row in Table 10). An alternative method would be to generate estimates of reach survivals for each of the four combinations of origin and group after multimodel averaging as suggested in Burnham and Anderson (1998), but the outcome of the two methods were nearly identical in this case. Point estimates of survival using the two methods were slightly different in the first reach, are identical thereafter, and confidence intervals from the two methods overlap considerably.

The estimates of apparent survival from the top model were similar in most reaches other than the first (Table 11). The point estimates ranged from 0.813 to 1.000 and the 95% confidence intervals were approximately $\pm 5\%$. The lowest point estimate was from the first reach (0.813, 95% CI 0.746-0.874), which is also the reach fish spent the most time within (release to Scott River). The greatest point estimate was in the fourth reach, Salmon River to Trinity River (1.000, 95% CI 0.963 to 1.000), a reach fish spent little time in. The estimate from this reach was 1.000 with little error, because every hatchery fish and every wild control fish that was detected at the head of that reach ($N = 75$ hatchery and 23 wild fish) was detected downstream of the reach, indicating no mortality. In addition, only 3 of 39 wild treatment fish detected at the head of the reach were undetected downstream.

The product of the reach survivals was used to estimate survival among reaches. The overall estimate of apparent survival from rkm 309 to rkm 33, taken as the product of

the individual reach estimates, was 0.653 (95% CI 0.578-0.729). It is important to realize the estimates for each reach were not scaled by the length of each reach and are therefore not directly comparable to one another on a length basis.

Table 11. Estimated apparent survivals and profile likelihood confidence intervals of radio-tagged hatchery and wild juvenile coho salmon in five study reaches of the Klamath River during spring, 2006. Results are based on data from 162 wild fish and 120 hatchery fish released from 25 April through 16 May 2006. Results are based on pooling fish of hatchery and wild origin and treatment and control groups. Data for the overall result was calculated as the product of the reach estimates with variance estimated using the delta method. Lengths from release to various sites are different for control and treatment groups.

Reach Description	Reach Length (km)	Apparent Survival	Standard Error	95% Confidence Interval	
				Lower	Upper
Release to Scott River	54 & 75	0.813	0.027	0.746	0.874
Scott River to Indian Creek	56	0.911	0.024	0.842	0.959
Indian Creek to Salmon River	71	0.929	0.020	0.872	0.968
Salmon River to Trinity River	38	1.000	7.8E-06	0.963	1.000
Trinity River to Steelhead Lodge	36	0.951	0.025	0.882	0.999
Release to Steelhead Lodge	255 & 276	0.653	0.039	0.578	0.729

Hatchery Only

Few of the models of survivals of hatchery fish were reasonably supported by the data from all release dates (4 April through 24 May 2006). The models included those in which survival could vary by several combinations of experimental group and reach, as in the analyses of hatchery and wild fish described earlier. A \hat{c} value of 1.437 was used to correct for overdispersion as described previously.

Only the model allowing survival to vary among reaches was reasonably supported by the data (Table 12). This model received approximately 3 times the weight of the Group + Reach model and 12 times the weight of model describing a difference in survival based on group in the first reach only (GroupAcute). Despite the similar weight of the reach only and Group + Reach models, the standard error of the beta coefficient for the group parameter of the latter model was over seven times larger than the beta

estimate, indicating it described an unimportant effect. Thus, we concluded the data did not support differences in survival between control and treatment experimental groups, and only the output from the most supported model need be examined.

Table 12. Model summary from analyses of apparent survival and capture probabilities of 211 radio-tagged hatchery juvenile coho salmon released from 4 April through 24 May 2006. Model descriptions include factors allowed to vary within apparent survival (Φ) and capture probabilities (P), including reach and group (treatment or control). GroupAcute denotes a model factor for an acute of group effect in the first reach only. Rankings are based on QAICc, a modification of Akaike Information Criterion for small samples and adjustments of extrabinomial variation. A '+' between factors indicates an additive effect. The global model includes multiplicative effects of all factors. Num. Params. denotes the number of estimable parameters in the model.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Params.	QDeviance
{ Φ (Reach), P(Reach)}	682.23	0.00	0.69	1.00	12	66.94
{ Φ (Group+Reach), P(Reach)}	684.27	2.03	0.25	0.36	13	66.91
{ Φ (GroupAcute), P(Reach)}	687.25	5.01	0.06	0.08	10	76.06
{global model}	699.81	17.58	0.00	0.00	22	63.70
{ Φ (.), P(Reach)}	708.91	26.68	0.00	0.00	7	103.85

The best supported model indicated the survival varied among reaches. The model indicates the survival was lowest in the first reach (0.786) and generally similar in all others (≥ 0.920 ; Table 13). This is consistent with the outcome of the analyses based on hatchery and wild fish described earlier. As in the hatchery and wild analysis, the effects of various covariates on survival were assessed based on this model.

Covariates of Reach Survival

Hatchery vs. Wild

Covariate models of hatchery-origin fish released on dates in common with wild fish had similar weights to one another and to the model without covariates, indicating little support for any of the three covariate hypotheses (Table 14). The models described weak relations between survival and the covariates, as indicated by 95% confidence intervals of the all slope parameter estimates overlapping zero. The models were not considered further based on these results.

Table 13. Estimated apparent survivals and profile likelihood confidence intervals of 211 radio-tagged hatchery juvenile coho salmon released from 4 April through 24 May 2006. Results are based on pooling fish of treatment and control groups. Data for the overall result was calculated as the product of the reach estimates with variance estimated using the delta method. Lengths from release to various sites are different for control and treatment groups.

Reach	Description	Reach Length (km)	Apparent Survival	Standard Error	95% Confidence Interval	
					Lower	Upper
----- Hatchery Origin -----						
1	Release to Scott River	54 & 75	0.786	0.029	0.714	0.850
2	Scott River to Indian Creek	56	0.925	0.023	0.860	0.967
3	Indian Creek to Salmon River	71	0.920	0.022	0.857	0.962
4	Salmon River to Trinity River	38	0.995	8.2E-03	0.960	1.000
5	Trinity River to Steelhead Lodge	36	0.975	0.016	0.924	1.000
Overall	Release to Steelhead Lodge	255&276	0.649	0.040	0.571	0.727

Covariate models of wild-origin fish were better supported by the data than the model without covariates, indicating support for several of the hypotheses. The Acute and Acute + Chronic models of the effects of temperature received 49% and 39% of the total weight, respectively, leaving the other models of temperature with little support by the data (Table 14). The moderate support for the Acute + Chronic model and poor support of the Chronic model (weight = 8%) suggests the Acute model is responsible for the support for the Acute + Chronic model, and therefore only the Acute hypothesis is a meaningful representation of the effect of temperature. The sign of the slope parameter of this temperature model (and the others) was negative and the 95% CI did not overlap zero; this model indicates a decrease in survival as temperature increased. The models of the effects of IGD discharge received slightly greater weight than the Time Only model, but no one covariate model was clearly better supported by the data than the others. The Chronic hypothesis (weight = 38%) was slightly more supported than the Acute hypothesis (weight = 17%), and is likely responsible for the support for the Acute + Chronic model; the support for this premise was less than that of the temperature model. The signs of the slope parameters of the Chronic and Acute + Chronic models were positive and that of the Acute model overlapped zero. The most supported models

Table 14. Results of time-dependent models [$\phi(t)$, $p(t)$] assessing the effects of covariates of survival along three hypotheses. The hypotheses for each covariate are A) an effect only between release and Scott river (Acute), B) an effect only downstream from the Scott River (Chronic), and C) the combination of both effects (Acute + Chronic). The data were based on 162 wild fish and 120 hatchery fish released from 25 April through 16 May 2006. A time-dependent model without covariates (Time Only) is presented to assess the relative improvement through the use of the covariates. The sign of the slope parameter is ‘?’ if the 95% CI overlapped zero.

Covariate	Hypothesis	QAICc	Delta QAICc	QAICc Weight	Model Likelihood	Number of Parameters	Slope Sign
----- Origin = Wild -----							
Temperature	Acute	701.88	0.00	0.49	1.00	13	-
Temperature	Chronic	705.60	3.72	0.08	0.16	13	-
Temperature	Acute + Chronic	702.35	0.47	0.39	0.79	13	-
None	Time Only	706.99	5.11	0.04	0.08	12	na
Discharge	Acute	705.97	1.57	0.17	0.46	13	?
Discharge	Chronic	704.40	0.00	0.38	1.00	13	+
Discharge	Acute + Chronic	704.57	0.17	0.35	0.92	13	+
None	Time Only	706.99	2.60	0.10	0.27	12	na
Date	Acute	703.50	0.00	0.51	1.00	13	-
Date	Chronic	707.07	3.57	0.09	0.17	13	?
Date	Acute + Chronic	704.45	0.94	0.32	0.62	13	-
None	Time Only	706.99	3.49	0.09	0.17	12	na
----- Origin = Hatchery -----							
Temperature	Acute	420.32	1.52	0.19	0.47	13	?
Temperature	Chronic	420.51	1.71	0.17	0.42	13	?
Temperature	Acute + Chronic	420.02	1.22	0.22	0.54	13	?
None	Time Only	418.80	0.00	0.41	1.00	12	na
Discharge	Acute	419.60	0.80	0.26	0.67	13	?
Discharge	Chronic	420.78	1.98	0.14	0.37	13	?
Discharge	Acute + Chronic	419.99	1.18	0.21	0.55	13	?
None	Time Only	418.80	0.00	0.39	1.00	12	na
Date	Acute	419.74	0.94	0.22	0.63	13	?
Date	Chronic	420.89	2.08	0.12	0.35	13	?
Date	Acute + Chronic	419.01	0.21	0.31	0.90	13	?
None	Time Only	418.80	0.00	0.35	1.00	12	na

indicate survival increased with discharge. An Acute effect was the most supported hypothesis of the effects of release date. As in the temperature model, the support of the Acute + Chronic model was likely due to the Acute effect, as the Chronic model was

poorly supported by the data (weight = 9%). The slope parameters of the Acute and Acute + Chronic models were negative, indicating survival decreased as release date increased.

Hatchery Only

The data including all hatchery releases supported several models of the effects of the covariates on survival. Acute effects of temperature and release date and chronic effects of discharge were best supported. Models of acute (model weight 55%) and chronic (weight 36%) effects of temperature received a total of 91% of the model weights of the temperature models (Table 15). The remaining models, Acute + Chronic and Time Only (no covariate effect), received little support. The sign of the beta coefficient of the Acute model was positive, and that of the Chronic model was negative. Based on these models, survival upstream from the Scott River increased with temperature and survival downstream from the Scott River decreased with temperature. Acute and Chronic models of the effects of discharge were reasonably supported by the data, receiving 10% and 80% of the total weights, respectively. The sign of the coefficient of the Chronic model was positive and those of the other models overlapped zero and were not considered. Thus, the overall effect was positive, indicating survival downstream from the Scott River increased with discharge, a result based on the Chronic model. The Acute model of the effects of release date was the only model of this covariate supported by the data, receiving 90% of the weight. The sign of the beta coefficient was positive, indicating survival upstream from the Scott River increased with release date.

Table 15. Results of time-dependent models [$\phi(t)$, $p(t)$] assessing the effects of covariates of survival along three hypotheses based on hatchery fish from all release dates. The hypotheses for each covariate are A) an effect only between release and Scott River (Acute), B) an effect only downstream from the Scott River (Chronic), and C) the combination of both effects (Acute + Chronic). The data were based on 211 hatchery fish released from 4 April through 24 May 2006. A time-dependent model without covariates (Time Only) is presented to assess the relative improvement through the use of the covariates. The sign of the slope parameter is ‘?’ if the 95% CI overlapped zero.

Covariate	Hypothesis	QAICc	Delta QAICc	QAICc Weight	Model Likelihood	Number of Parameters	Slope Sign
----- Origin = Hatchery -----							
Temperature	Acute	677.92	0.00	0.55	1.00	13	+
Temperature	Chronic	678.78	0.86	0.36	0.65	13	-
Temperature	Acute + Chronic	683.86	5.95	0.03	0.05	13	?
None	Time Only	682.23	4.32	0.06	0.12	12	na
Discharge	Acute	681.50	4.13	0.10	0.13	13	?
Discharge	Chronic	677.37	0.00	0.80	1.00	13	+
Discharge	Acute + Chronic	684.27	6.90	0.03	0.03	13	?
None	Time Only	682.23	4.86	0.07	0.09	12	na
Date	Acute	676.71	0.00	0.90	1.00	13	+
Date	Chronic	684.22	7.51	0.02	0.02	13	?
Date	Acute + Chronic	684.00	7.29	0.02	0.03	13	?
None	Time Only	682.23	5.52	0.06	0.06	12	na

DISCUSSION

The results of migration analyses from this study are similar to those from the 2005 study by Stutzer et al. (2006). Both studies found longer travel times from release to the Scott River than in reaches farther downstream. Each study also found discharge was a significant covariate of migration in this reach and not in others, despite using different analytical methods (linear regression vs. Cox proportional hazards regression). Stutzer et al. (2006) found a weak positive relation between migration rate and discharge for wild fish in this reach and we found a weakly negative one for wild fish and a strongly

negative one for hatchery fish, though the discharges were quite different during the two studies. The relations between day of the year, water temperature, fish length, and travel rate were similar in the two studies, with each noting faster downstream travel as these variables increased. Stutzer et al. (2006) found locations of radio-tagged juvenile coho salmon were primarily within 6 m of shore near shear zones with overhead or no cover along the edges of pools in the main river channel. The association of juvenile coho salmon with shoreline areas is consistent with many other studies. The absence of cover at many fish locations in 2005 is contrary to our supposition that fish did not move downstream during the highest discharges in 2006 due to their association with cover. However, in 2006 the Klamath River had a higher discharge than in 2005 which inundated many areas that were dry in 2005 resulting in more cover. Stutzer et al. (2006) also found wild fish migrated from release to the Scott River faster than hatchery fish as we did, though their comparison was of few fish released on different dates.

The data from this first year of study indicated there were differences between hatchery and wild fish migration behaviors in the upper two reaches (upstream from Indian Creek at rkm 178), but not thereafter. Fish origin was a significant covariate of travel time through these reaches, with wild fish traveling faster than hatchery fish. Variables representing discharge, water temperature, and release date were also significant covariates of travel time through the first reach (IGH to Scott River), but they were correlated with one another and their effects could not be separated in the models. The travel time in the first reach was reduced as the discharge decreased, water temperature increased, and day of the year increased as the study season progressed.

The difference in travel times of hatchery and wild fish in the first reach diminished over time. The difference between origins was caused by a difference in the time between release and migration between hatchery and wild fish. Travel times of hatchery and wild fish through reaches three and greater (downstream from Indian Creek) were similar, but the effects of the different times hatchery and wild fish spent in the first reach persisted as they passed the last detection site at rkm 13. These differences may be as much the differences between naïve fish vs. migrants as they are between hatchery fish

and wild ones. Differences between hatchery and wild fish are commonly attributed to differences in the physiological status, or “readiness to migrate” between fish of the two origins. The ATPase levels of wild fish were statistically greater than hatchery fish, which is consistent with this premise. The ATPase activities of hatchery fish showed little trend over time and those of wild fish increased slightly over time, indicating little change in the levels of smoltification at the time of tagging over the course of the study. Condition factor is often associated with changes in smoltification, but did not show a trend over time in hatchery or wild fish (at the time of tagging). The condition factor of wild and hatchery fish were generally similar (data not shown), but comparisons between fish from such diverse prior histories may not be an appropriate means of assessing smoltification. The reduction in the ‘migration delay’ of the naïve hatchery fish over time may have been caused by changes in photoperiod and water temperature, as well as the time in the river after release, as these factors have been shown to affect the rate of smoltification of several salmonid species (Zaugg 1985; McCormick et al. 1987; Beeman et al. 1994; Muir et al. 1994). Change in photoperiod is generally believed to be the proximate factor indicating the migration season to juvenile salmonids and temperature is believed to be a mediator of the rate of smoltification, influencing response to discharge (Jonsson 1991; Quinn 2005). However, the factors affecting migration in streams are not well understood. Ewing et al. (1980) found migration of juvenile Chinook salmon in the Rogue River of southern Oregon without elevated ATPase activities. They attributed initiation of migration to high river discharge and concluded elevated ATPase activities are often associated with migration, but are not a prerequisite for it.

Discharge was a significant covariate of travel times through Reach 1, but the effect size was different in wild and hatchery fish. Travel times of hatchery fish through Reach 1 were longer than those of wild fish and decreased throughout the study period. Regression analyses indicated effects of discharge on wild fish were small, resulting in a predicted increase in median travel time of about 5% at discharges of 4,770 cfs compared to 6,002 cfs, whereas the predicted median travel time of hatchery fish would increase by 181%. Individual models based on the current data indicate discharge, water

temperature, and date were significant contributors to migration, but their effects could not be separated due to correlations between them.

The data and models indicate travel time increases with discharge, which is contrary to the commonly accepted notion of discharge increasing migration rates. However, much of the literature describing the relation between discharge and migration rate is from studies of actively-migrating juvenile salmonids in large river systems (Raymond 1968; Berggren and Filardo 1993; Giorgi et al., 1997; Smith et al., 2002). These often do not represent fish or environmental conditions in smaller rivers and may not be applicable to the Klamath River. The process of downstream migration of juvenile coho salmon is generally believed to be triggered by photoperiod and mediated by water temperature and discharge (Sandercock 1991; Quinn 2005). The timing of downstream migration is generally later in cool water years, presumably due to slower growth and physiological development under these conditions. The conditions in the Klamath River Basin during the winter of 2005/2006 were characterized by cooler than average temperatures and greater than average discharge. It is possible that the cool water conditions resulted in slow growth and physiological development, resulting in a resistance to downstream migration during the high discharge present early in the study period and an increase in migratory tendencies as water temperatures increased, day lengths increased, and discharge decreased. The affinity of juvenile coho salmon for woody debris as cover habitat during downstream migration and smoltification described by McMahon and Holtby (1992) is consistent with the lack of migration during the high discharges during our study period. We could not determine if the inverse relation between travel time and discharge was a true causal effect, or if it was simply a correlation. Potential explanations include high discharge: 1) inundating new shoreline habitat and providing refuge areas for juvenile salmonids, 2) altering the relation between river cross section and water velocity, and 3) occurring in 2006 during the early spring when the hatchery fish were not 'ready' to migrate. Each of these, and potentially other, hypotheses may have merit.

The data and models do not support clear differences between survival of wild and hatchery fish, but considerable model uncertainty exists. Model uncertainty means the ‘best’ model from this analysis might not remain the ‘best’ model if the experiment were repeated, and indicates the models, given the data, are insufficient to distinguish among the various factors. A model without differences in origins was the top-ranked model, but its rank was only about 2.6 times that of the model allowing survival to vary by origin, which indicated either model was plausible given the data. Burnham and Anderson (1998) suggested model weights differing by a factor of at least seven indicate meaningful differences between models. Based on their general recommendation, four models in the current hatchery vs. wild survival analysis appear plausible: no origin effect, an effect of the experimental group in the first reach, an overall origin effect, and the combination of the latter two. In many analysis methods only the ‘best’ model is considered and model uncertainty is not addressed. In the present analysis, that approach would indicate there are no differences in survival between hatchery and wild fish, which is an uninformed representation of the data. Thus, the current data and models neither support nor refute differences in survival between hatchery and wild fish. Inasmuch as the 2006 study was conducted during a very wet period characterized by high river discharges and low water temperatures relative to other years, this outcome may be different in other water year types.

The overall (pooling origins and groups) estimates of survival were similar in most reaches other than the first. The lowest estimates were between Iron Gate Hatchery and the Scott River (0.813) and the highest were between the Salmon and Trinity rivers (1.000). The fish spent the most time between the hatchery and Scott River and the least between the Salmon and Trinity rivers. The low survival and long travel times in the first reach relative to the others suggests: 1) survival is dependent on the time fish spend within a reach and not just the length of the reach, and/or 2) the conditions in the first reach are such that survival there is inherently lower than in the others.

The survival per unit distance from Iron Gate Hatchery to the Shasta River (21 km) was higher than from the Shasta River to the Scott River (54 km). An analysis of pooled

hatchery and wild treatment fish indicate estimated survivals of 0.979 (95% CI 0.911 to 1.000) from Iron Gate Hatchery to the Shasta River and 0.860 (95% CI 0.764 to 0.937) from the Shasta River to the Scott River (data not shown). These estimates are equivalent to survivals of 0.904 per 100 km from the hatchery to the Shasta River and 0.756 per 100 km from the Shasta River to the Scott River. The latter estimate is similar to the control fish estimates per 100 km through the same reach (0.651 hatchery and 0.791 wild), and indicates the survival of treatment and control groups were both low in this area relative to the hatchery to Shasta River area.

The estimate of the overall survival from Iron Gate Hatchery to rkm 33 indicated survival through this reach of the Klamath River in 2006 was similar to survival in other rivers. The survival over this 276 km distance was 0.653 (from Table 11), which equates to a survival of 0.857 per 100 km. The current data suggest survival may not be constant through the various reaches of the Klamath River, but this approach is useful for purposes of comparison. Cramer Fish Sciences (2007) compiled a variety of survival data and reported survivals of juvenile Chinook salmon from Snake River hatcheries traveling between the hatcheries and Lower Granite Dam ranged from 0.622 to 0.949 per 100 km during 1993 to 2003. Estimates from coho salmon in the Yakima River were available from 1999, 2001, and 2003 and were 0.913, 0.790, and 0.834 per 100 km, respectively (Cramer Fish Sciences 2007).

There were both differences and similarities in the analyses of the effects of covariates on survivals of hatchery and wild fish. The models of covariate effects based on hatchery and wild fish released on common dates indicated effects on wild fish survival that were not supported in data from hatchery fish. However, when the entire suite of hatchery fish releases were used the results of the analyses were in some respects similar to those based on wild fish. In both instances, the effects of temperature and release date were primarily in the first reach, where they spent most of their time. The signs of the effects (positive or negative) of these covariates differed among the fish origins, presumably due to differences in their migrations in the first reach. The effects of IGD discharge on survivals of hatchery and wild fish were generally similar (positive

relation), and the effects on hatchery, and to a lesser extent wild, fish were largely downstream from the Scott River. This is likely due to the long residence of hatchery fish between release and the Scott River relative to wild fish. Inasmuch as the differences between hatchery and wild fish we observed were likely those of migrants vs. non-migrants, the use of hatchery fish captured as they are migrating downstream, rather than those from hatchery tanks, may increase similarities between hatchery and wild fish in future studies.

We believe the reasons for the hatchery-wild covariate differences are due to the differences in their migration behaviors in the first reach. As noted previously, many hatchery fish remained upstream from the Scott River for weeks (prior to the 2 May release date), whereas wild fish spent relatively little time in this reach (after the 18 April release date). The trend of a decrease in time in this reach as release date progressed was common in hatchery and wild fish, but the magnitude was much greater in the hatchery fish. We hypothesize that survival is negatively related to exposure time to mortality factors, and that the different amounts of time hatchery and wild fish spent in the first reach accounts for the difference in covariate effects between them. If true, this hypothesis would explain the differences in the effects of temperature and release date between wild and hatchery fish. Under this hypothesis, the decreasing amount of time hatchery fish spent in the first reach as release date progressed and temperature increased would result in greater survival later in the study, which is consistent with the weighting of the models.

The common effect of discharge on survivals of hatchery and wild fish may be explained by examining the model support for the hatchery-only models describing the effects of discharge. The Chronic model, describing an effect of discharge after the hatchery fish had left the first reach, was most supported by the data (weight = 80%). This model was not affected by the long residence times in the first reach and described an effect of discharge in portions of the study area in which hatchery and wild fish had similar migration characteristics. The Chronic model was also the most supported hypothesis of wild fish (model weight = 0.38), but there was considerable model uncertainty in results from wild fish.

The positive relation between IGD discharge and survival downstream from the Scott River does not indicate causation between these variables. Due to the wet water year in 2006, discharge at IGD was typically greater than its hydraulic capacity and the dam did not usually regulate river discharge. As such, the discharge of the Klamath River at the dam was correlated with the discharges of many Klamath River tributaries downstream, resulting in high tributary discharges during periods of high discharge at the dam. In addition, the proportion of river discharge contributed by the dam diminished as tributaries merged into the main stem river. Thus, the positive relation between discharge and survival in 2006 may describe an overall effect, rather than an effect specifically from discharge at the dam. This pattern may be different during a drier water year type, particularly if the current minimum discharges mandated by the Biological Opinion were used. A study design with experimental dam discharges could examine the question of causation.

After this first year of research the fishery managers are left with the difficult decision of how to evaluate the effects of IGD discharge on the SONCC ESU of coho salmon. Wild fish are generally in short supply in two of every three years. This ESU includes both hatchery and wild fish, indicating studies of each would be prudent. However, the delay between release of fish taken directly from the hatchery and their migration appears to be the cause of differences in the effects of discharge and survival in the IGD to Scott River reach, indicating naïve hatchery fish are not suitable surrogates for wild fish using this release strategy. The cause of this delay is likely due to differences in physiological development of hatchery and wild fish, and some indication of this was evident in ATPase activities during this study. The sentinel studies we conducted did not increase ATPase activities appreciably, and those methods would probably not be sufficient to change the behaviors of hatchery fish shortly thereafter. However, the water source of the hatchery (Iron Gate Reservoir) and Klamath River near the hatchery are the same, and placing hatchery fish in a water source not as familiar may result in a greater effect. Studies of the effects of novel water on smoltification support this premise (Hoffnagle and Fivizanni 1990). We will evaluate this approach in 2007 by taking untagged fish from the hatchery and holding them in the Shasta River prior to measuring their ATPase

activities. Other alternatives include holding fish in the Klamath River for an extended time prior to tagging, using hatchery fish captured in migrant traps in the Klamath River, and releasing hatchery fish in the Shasta River and collecting migrants at the trap used as the source for wild fish in this study. These approaches could result in hatchery “migrants” being used in the study rather than hatchery “non-migrants”, but the latter alternative may be undesirable to fishery managers for other reasons.

In summary, differences in migration rates of wild and hatchery fish were present in some areas, but no clear difference in their overall survival was evident from this first year of study. River discharge, water temperature, and day of the year were significant predictors of travel time between Iron Gate Hatchery (rkm 309) and the Scott River (rkm 234), but not in reaches farther downstream. Their effects could not be separated due to correlations between them. A design including experimental river discharges could correct this problem in future studies. The relations between survival and the covariates temperature, release date, and IGD discharge were different among hatchery and wild fish upstream from the Scott River. The survival of hatchery and wild fish downstream from the Scott River was positively related to discharge at the dam. The current data do not support the use of naïve hatchery fish as surrogates for migrant wild fish to determine the effects of discharge on survival of wild fish upstream from the Scott River, yet studies of hatchery as well as wild fish may be prudent given their inclusion in the SONCC ESU.

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Appendix 1. Tag life test.

Introduction

An assumption of release-recapture models used to estimate survival is that all live tagged individuals have the same probability of being detected at downstream detection arrays. Since radio transmitters (tags) have a limited and varied battery life, the tag failure rate may affect detection probabilities, depending on travel time of a tagged fish and the time a tag is on prior to release. Thus, survival estimates may be negatively biased if the tag expires prior to a fish passing all the detection arrays. Information obtained by a tag-life study can be used to adjust survival estimates using the probability that a tag will expire prior to fish exiting the study area (Townsend et al. 2006; Cowen and Schwarz 2005).

Methods

We used the methods of Townsend et al. (2006) to conduct a tag-life study to estimate the probability that a tag was operating when passing our detection arrays. The tag-life study entailed activating tags during the study period, and monitoring tag failure over time. We randomly selected 25 model NTC-M-2 tags from the pool of tags to be deployed in the survival study, making sure to represent the four frequencies (channels) equally. Tags were activated, submerged in water, and monitored with a Lotek SRX-400 data logging receiver. The expiration time was determined by the last record of detection of each tag.

Tag-life data were used to model tag survivorship and for calculating the probability of a tag being operational at each detection array as per Townsend et al. (2006). The tag-life data were fit to a Gompertz distribution (Elandt-Johnson and Johnson 1980). A non-parametric form of the tag survival function was used because travel times of radio-tagged salmonids are typically highly skewed (i.e., data are not normally distributed). Tag-life data were ranked to facilitate the estimation of model parameters. The Gompertz survival distribution function takes the form

$$S(t) = e^{(\beta/\alpha)(1-e^{-\alpha t})}$$

where $S(t)$ is the probability the radio-tag is operational at time t and parameters α and β are to be estimated by fitting the model to the tag-life data.

Travel time to different detection arrays were then substituted into this function for estimating the probability a tag was operating when a fish arrived at a particular detection array. During our tagging procedures, tags were turned on prior to release (approximately 18-36 hours), so the elapsed time a tag was operating before release was added to travel times.

Results and Discussion

The period that the tags were operational generally exceeded the minimum battery life (45 d for the model NTC-M-2) specified by the manufacturer. Three of the 25 tags tested expired prior to the specified 45 days. The first premature tag failure occurred at 10.6 d, the second at 23.9 d, and the third at 33.9 d. The operational period of the remaining 22 tags ranged for 46.4 to 81.5 d. The mean operational period was 60.1 d.

The tag-life study was analyzed for generating model parameters of the Gompertz distribution and calculating probabilities radio-tags were alive at detection arrays. Our tag-life data fit well with the Gompertz survival distribution function (Figure 1) allowing us to use this model for calculating probabilities. Parameter estimates were $\alpha = 0.094$ ($SE = 0.0248$), $\beta = 0.157 \times 10^{-3}$ ($SE = 0.220 \times 10^{-3}$), and $R^2 = 0.874$.

We determined that the probability of a tag being operational at downstream arrays was high, with all probabilities greater than 98 % (Table 1). The cumulative arrival distributions plotted with the Gompertz model over time shows that tagged coho salmon passed through downstream detection arrays before tag-failure was substantial (Figure 2). Since the probability of a tag being operational at the downstream detection arrays for our survival studies was very close to one (Table 1), we did not adjust our survival estimates.

Table 1. Estimated probabilities (mean, SD in parentheses) that a radio-tag was operational at downstream detection arrays, during 2006.

Detection Array Locations	Release Sites	
	Iron Gate Dam (test)	Shasta River (control)
Shasta River	0.996 (0.012)	n/a
Scott River	0.991 (0.016)	0.994 (0.009)
Indian Creek	0.983 (0.068)	0.991 (0.028)
Salmon River	0.985 (0.022)	0.990 (0.014)
Trinity River	0.985 (0.022)	0.990 (0.015)
Steelhead Lodge	0.974 (0.076)	0.987 (0.017)
Blake's Riffle	0.964 (0.119)	0.981 (0.086)

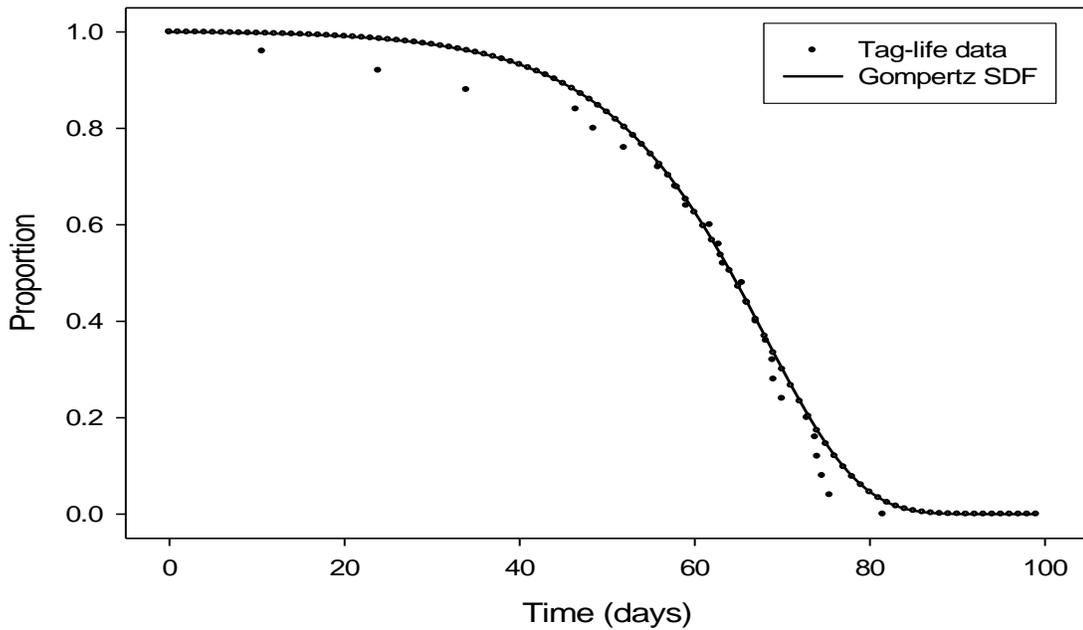


Figure 1. The Gompertz survival distribution function fit to the tag-life data.

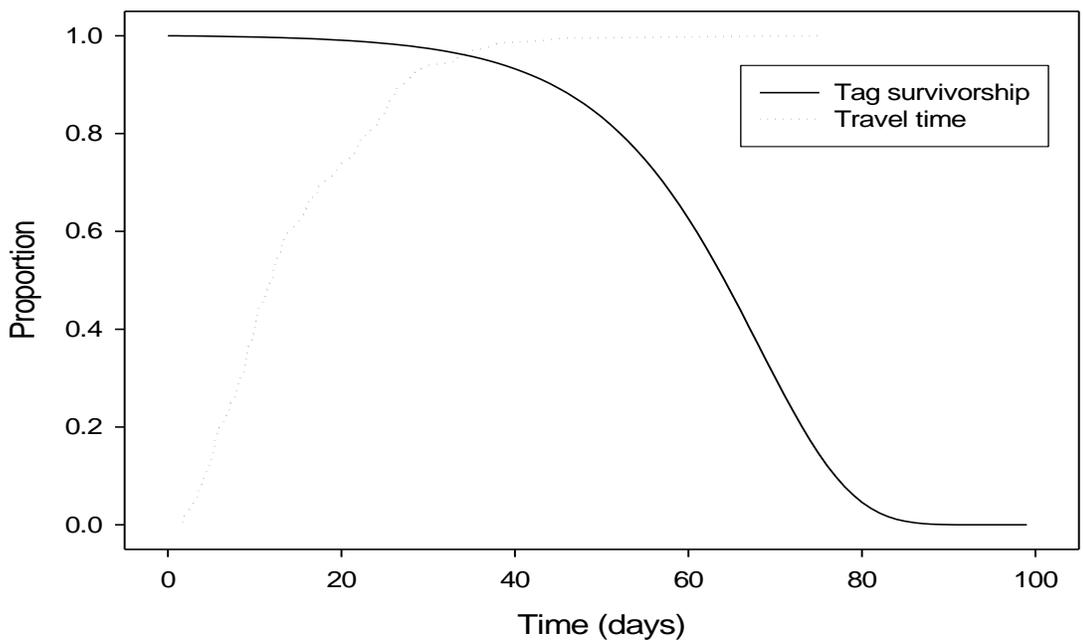


Figure 2. Cumulative travel time distribution of tags (dotted line) compared to survival distribution function for tag battery life (solid line) for 2006. Travel time distributions include the total elapsed time that the tag was operating prior to release of fish.

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Appendix 2. BKD sampling results.

Results of the qualitative nested PCR (Method 1) and the quantitative qPCR (Method 2) tests to determine prevalence of bacterial kidney disease. Samples were taken at Iron Gate Hatchery, on 24 May 2006.

Sample Number	Sample Weight (mg)	DNA Concentration (ng/ μ L)	Method 1	Method 2			
			Nested PCR	qPCR			Total Bacteria per mg Tissue
				Count Mean	Quantity Mean*	Number of Bacteria in Total Extraction**	
01	6.1	10	neg		0	0	0
02	6.2	130	neg		0	0	0
03	4.5	70	neg	37.6	1	113	25
04	8.4	110	neg		0	0	0
05	7.6	30	neg	37.1	3	211	28
06	5.4	70	pos		0	0	0
07	9.8	110	neg		0	0	0
08	6.1	130	neg		0	0	0
09	6.8	80	pos		0	0	0
10	6.7	70	neg		0	0	0
11	1	40	neg		0	0	0
12	8.8	60	neg		0	0	0
13	7.2	80	neg		0	0	0
14	6.9	110	neg		0	0	0
15	4.3	90	pos	32.8	39	3125	727
16	2.7	60	neg		0	0	0
17	9.8	20	pos	35.2	8	678	69
18	4	20	neg	37.3	2	179	45
19	9.6	30	neg		0	0	0
20	10.5	50	pos	35.8	6	474	45
21	7.3	40	neg	36.7	3	273	37
22	10	130	neg		0	0	0
23	10.6	170	neg		0	0	0
24	9.9	90	pos		0	0	0
25	6.9	60	neg		0	0	0
26	7.7	80	neg		0	0	0
27	5.6	40	neg		0	0	0
28	4.7	50	neg	38.1	1	79	17
29	5.4	190	neg		0	0	0
30	6.2	60	neg		0	0	0
31	10.1	40	neg		0	0	0
32	4.9	60	pos	38.3	1	98	20
33	6.3	70	neg		0	0	0
34	8.6	90	neg	36.9	3	202	24
35	9.1	100	neg		0	0	0
36	6.1	50	neg		0	0	0
37	11.2	130	neg		0	0	0
38	8.8	120	neg		0	0	0
39	5.8	90	neg		0	0	0
40	12.2	180	neg		0	0	0
41	6.7	70	neg		0	0	0
42	13.5	30	neg		0	0	0
43	12.3	130	neg		0	0	0
44	8.1	90	neg		0	0	0

Appendix 3. Capture histories from hatchery vs. wild analyses.

Capture histories of hatchery and wild fish release from 25 April through 16 May 2006. Histories begin with '1' for release and are '1' if they were detected and '0' if they were not at Scott River, Indian Creek, Salmon River, Trinity River, Steelhead Lodge, and Blake's Riffle, California.

Capture History	Hatchery Control Observed	Hatchery Treatment Observed	Wild Control Observed	Wild Treatment Observed
1111111	24	24	10	7
1111110	2	1	0	3
1111101	0	1	2	4
1111100	1	2	0	4
1111011	3	2	1	1
1111010	1	0	0	0
1111001	0	0	0	1
1111000	0	0	0	1
1110111	2	2	1	1
1110110	1	0	0	1
1110101	0	0	6	3
1110100	0	0	0	2
1110011	0	0	0	1
1110010	0	0	1	0
1110001	0	0	2	0
1110000	2	2	0	1
1101110	0	1	0	0
1101011	0	0	1	0
1100011	0	0	0	1
1100001	0	0	0	1
1100000	1	5	2	6
1011111	5	4	6	9
1011110	1	0	0	1
1011101	0	0	1	3
1011100	1	0	1	0
1011011	0	0	1	0
1011001	1	0	0	2
1011000	0	0	0	1
1010111	0	0	3	2
1010110	0	0	1	0
1010101	0	1	5	0
1010100	0	0	0	1
1010011	0	0	0	1
1010001	0	0	3	3
1010000	0	2	4	3
1001111	0	0	0	1
1001110	0	1	0	0
1001000	0	0	0	1
1000110	0	0	1	0
1000100	0	0	2	1
1000010	0	0	0	2
1000001	0	1	3	0
1000000	12	14	19	11

Appendix 4. Capture histories of hatchery fish from all releases.

Capture histories of hatchery from 4 April through 24 May 2006. Histories begin with '1' for release and are '1' if they were detected and '0' if they were not at Scott River, Indian Creek, Salmon River, Trinity River, Steelhead Lodge, and Blake's Riffle, California

Capture History	Hatchery Control	Hatchery Treatment
	Observed	Observed
1111111	39	47
1111110	3	2
1111101	1	2
1111100	1	2
1111011	4	2
1111010	1	1
1111000	1	0
1110111	3	6
1110110	1	0
1110011	0	1
1110001	1	0
1110000	6	3
1101110	0	1
1100101	1	0
1100001	0	1
1100000	4	7
1011111	7	5
1011110	1	0
1011101	0	1
1011100	1	0
1011011	0	1
1011001	1	0
1010101	0	1
1010000	0	3
1001110	0	1
1000001	0	1
1000000	21	26

Appendix 5. Paired release model results (wild coho).

Table of model results of wild coho salmon from the paired-release design. Final analyses were based on model-averaged results. See Burnham et al. (1987) for model definitions.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Par	QDeviance
{H1phi}	725.38	0.00	0.35	1.00	13	103.35
{Ho}	725.60	0.22	0.32	0.90	12	105.67
{H2p}	726.66	1.28	0.19	0.53	14	102.52
{H2phi}	728.19	2.81	0.09	0.25	15	101.93
{H3p}	730.26	4.87	0.03	0.09	16	101.87
{H4p}	731.33	5.94	0.02	0.05	18	98.67
{H3phi}	732.39	7.00	0.01	0.03	17	101.87

Appendix 6. Paired release model results (hatchery coho).

Table of model results of hatchery coho salmon from the paired-release design. Final analyses were based on model-averaged results. See Burnham et al. (1987) for model definitions.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Par	QDeviance
{H1phi}	395.01	0.00	0.40	1.00	12	46.69
{Ho}	395.03	0.02	0.40	0.99	12	46.70
{H3p}	398.64	3.63	0.07	0.16	16	41.83
{H2p}	399.23	4.22	0.05	0.12	14	46.68
{H2phi}	399.43	4.42	0.04	0.11	15	44.76
{H3phi}	400.17	5.16	0.03	0.08	17	41.22
{H4p}	402.18	7.16	0.01	0.03	18	41.08