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Arcata Fisheries Technical Report TR2006-05

An Initial Assessment of Radio Telemetry for Estimating Juvenile Coho Salmon Survival, Migration Behavior, and Habitat Use in Response to Iron Gate Dam Discharge on the Klamath River, California.

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Abstract. We surgically implanted radio transmitters into 80 wild coho salmon smolts captured emigrating from two tributaries into the Klamath River and 96 hatchery coho salmon smolts obtained from Iron Gate Hatchery during spring 2005 to improve our understanding of smolt survival and migration behavior under proposed Klamath River Project flows. A primary objective of the study was to determine the efficacy of using automated radio telemetry arrays to estimate smolt survival within the mainstem Klamath River. We also investigated the extent that various factors influenced the downstream migration rate of juvenile wild and hatchery coho salmon through four index flow reaches located between Iron Gate Dam (IGD) and the estuary. Migration rates were analyzed using bivariate and multiple-regression models. The dependent variable was the rate (km/d) at which radio-tagged smolts migrated downstream from release sites near IGD. Predictor variables consisted of indices of river discharge volume (flow) and surrogate indices of smoltification including photoperiod, river temperature, fish length, and release date. Additionally, we identified and compared mainstem river habitat types occupied by wild and hatchery coho salmon smolts during daylight hours.

Capture probability estimates for fish passing arrays were high (≥ 0.84), demonstrating that radio-telemetry can effectively be used to estimate survival of emigrating juvenile coho salmon in the Klamath River. Median migration rates increased as fish traveled downstream through reaches of increasingly higher flow volume, but were highly variable. Regression analyses did not reveal a clear pattern of correlation with any single or combination of predictor variables for any of the four index flow reaches. Both hatchery and wild tagged coho salmon were located in various meso-habitat types, but were found most frequently in low-velocity pools adjacent to shear zones. The majority of fish movements we observed did not meet the stringent criteria we established *a priori* to define mainstem rearing behavior. Eleven percent of wild and 4% of hatchery coho salmon we tagged were categorized as rearing in the mainstem river in spring and early summer, prior to continuing their migration to the estuary. However, proportions of tagged fish identified as rearing were likely underestimated by the criteria we used to define rearing behavior. Results from this study were used to develop the experimental design for a study being conducted in 2006 to estimate juvenile coho salmon survival relative to IGD flow releases.

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, Frissell 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.

Maintenance and restoration of anadromous fish populations requires sufficient streamflows to provide adequate habitat for spawning and rearing throughout the freshwater phase of their life cycle, as well as during the emigration of juvenile fish to the ocean (Cada et al. 1997). Coho salmon evolved in free-flowing rivers in which downstream migration of smolts was often associated with high spring streamflows. 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 smolts and decrease smolt survival by increasing exposure to predation and disease (Cada et al. 1997, Clements and Schreck 2003). Additionally, delayed migration may impair osmoregulatory ability of smolts entering the marine environment (Berggren and Filardo 1993).

In an effort to lessen negative effects associated with delayed migration, regional managers in the Columbia River Basin have developed water management strategies to increase water velocity, principally through flow augmentation. The intent is to increase water velocity and smolt migration rates sufficiently to provide appreciable gains in smolt survival at ocean entry. Flow augmentation is the principal tool being employed in the recovery of Snake River salmon populations listed as threatened or endangered under the Endangered Species Act (NMFS 1995).

In consultation with the NMFS and the U.S. Fish and Wildlife Service (FWS), the Bureau of Reclamation (BOR) developed a Ten Year Operations Plan that proposed to “divert, store and deliver (from storage) Klamath Project (Project) water consistent with applicable law” from the upper Klamath River Basin (NMFS 2002). Flow conditions from Bogus Creek to at least the Scott River are significantly influenced by the volume of water released from Iron Gate Dam (IGD). In their 2002 Biological Opinion, NMFS determined that the Project was likely to jeopardize the continued existence of coho salmon and result in the adverse modification of designated critical habitat of coho salmon. In their reasonable and prudent alternative (RPA) to BOR’s proposed action, NMFS required BOR to continue to refine the RPA target flows by, in part, implementing scientific studies to determine what effect different spring IGD flow regimes have on survivorship of coho salmon smolts during outmigration.

Factors affecting coho salmon smolt migration, survival, and habitat preference during varying flow regimes on the Klamath River are largely unknown. The limited abundance of coho salmon smolts within the mainstem 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 smolt 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, Clements and Schreck 2003) for several salmonid species.

Studies on various salmonid species on the Columbia River have provided evidence that the migration rate of smolts through impoundments is positively related to water velocity (Berggren and Filardo 1993, Giorgi et al. 1997). 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.

The objectives of this first year study were to (1) determine the efficacy and sample size requirements for subsequent formal studies evaluating the relationship between flow and survival of coho salmon smolts within the mainstem Klamath River using automated radio telemetry arrays; (2) describe the migratory characteristics of wild and hatchery coho salmon smolts through four river index reaches to identify variables that influence migration rate and assess the strength and implications of those relationships; and (3) identify and compare mainstem river habitat use by wild and hatchery coho salmon smolts during daylight hours.

STUDY AREA

The Klamath River and its watershed encompass more than 40,403 km^2 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 largest in the contiguous United States, give way to more Mediterranean conditions and vegetation in the middle and upper watershed.

The study area encompassed 310 river kilometers (rkm) of the mainstem Klamath River from IGD to the estuary near the mouth at the Pacific Ocean (Figure 1). Fixed radio telemetry arrays were located near the confluences of major tributaries and above the estuary. The reach from Bogus Creek (rkm 309.5) to the Scott River (rkm 234) is significantly influenced by IGD flow releases and was studied intensively to address objectives 2 and 3 (Figure 2).

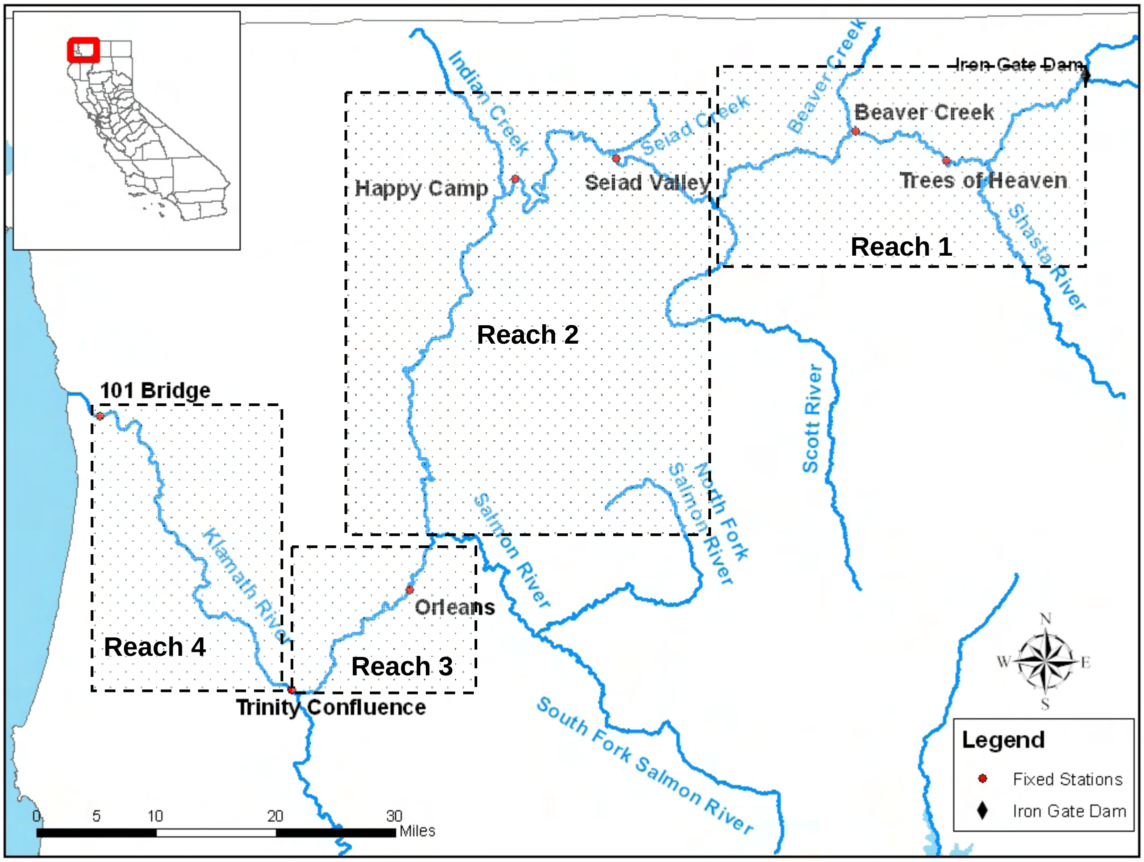

Figure 1. Map of the Klamath River study area showing tributaries delineating index reaches and locations of automated radio telemetry arrays.

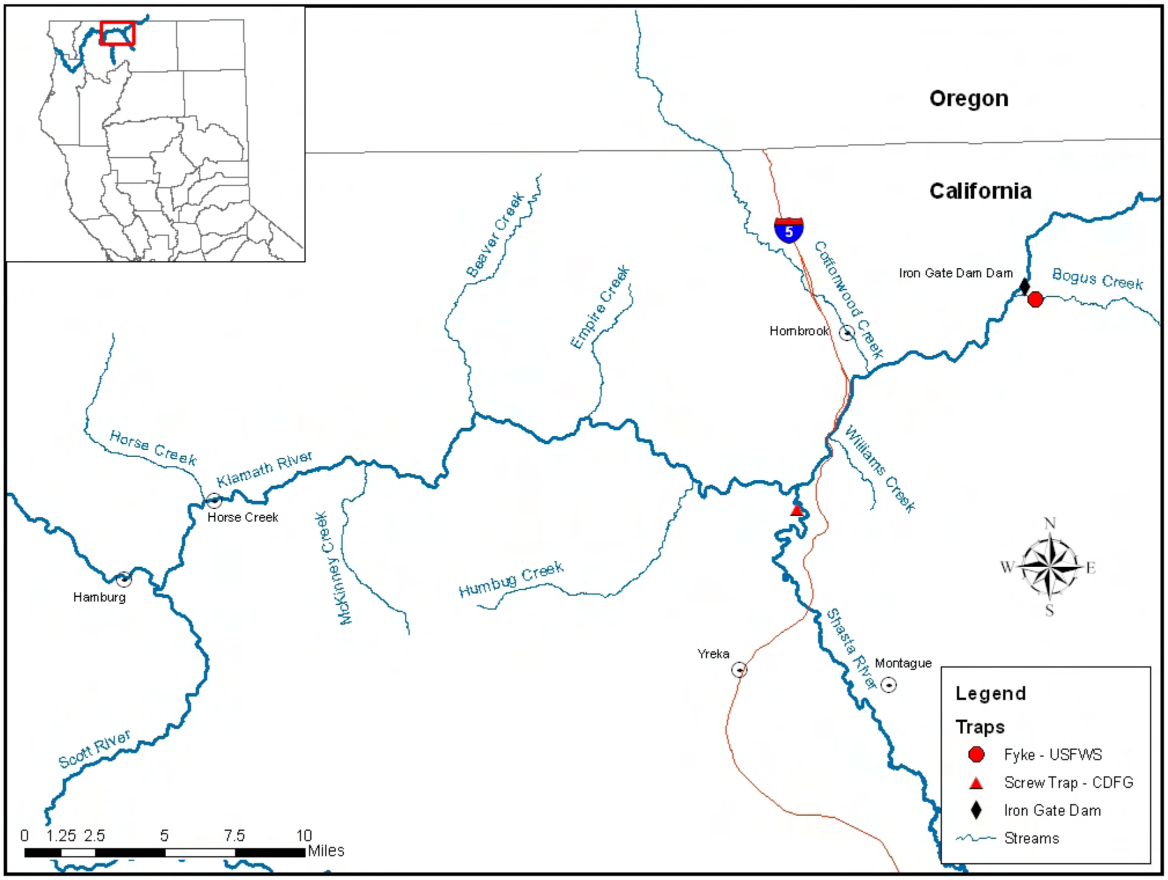

Figure 2. Upper mainstem Klamath River study area and location of fish collection and tagging sites at Bogus Creek and Shasta River.

METHODS

Transmitter specifications

Pulse-coded radio transmitters used in this study were developed by Lotek Wireless, Inc (Newmarket Ont.). Transmitter dimensions (model NTC-M-2 nano-tag) were 5.6 mm wide by 3.7 mm high by 13.7 mm in length and weighed 0.5 g in air. The antenna measured 0.5 mm by 24 cm and was covered in a Teflon coating. Four groups of transmitters operating on separate frequencies between 148.320 and 151.320 MHz were used. Within each frequency, transmitters were differentiated into four subgroups based on the burst rate of their uniquely coded radio signal (7.9, 8.0, 8.1, and 8.2 s.). The expected life of transmitters used in this study was 32 d.

Fish collection and surgical procedures

Coho salmon smolts were collected for tag implantation at Bogus Creek, the Shasta River, and Iron Gate State Fish Hatchery (IGH) (Figure 2). Wild coho salmon smolts were collected from downstream migrant traps located near the confluences of Bogus Creek and Shasta River with the mainstem Klamath River from 1 March through 5 May, 2005. Coho salmon smolts from IGH were tagged from 20 April through 2 June. Fish (115-213 mm FL) obtained from IGH were transferred from outdoor raceways into a large outdoor circular tank (1,400 L; 1.5 m in diameter, 0.9 m deep) on 12 April, 2005. We selected hatchery fish within this size range to be representative of the size range of wild coho salmon smolts collected from Bogus Creek and the Shasta River that were implanted with radio transmitters.

Procedures for surgical implantation of radio transmitters were similar to those described by (Adams et al. 1998a). 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® to support the fish's body during surgery. 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 near 250 mL/min through a tube placed in the fish's mouth for the duration of the procedure. The mean (± SD) time to complete each surgical procedure was 3 min 12 s (± 26 s).

Prior to insertion, transmitters were sterilized by soaking for 24 h in a cold sterilization solution of 3.4% glutaraldehyde (Cidexplus®) then rinsed with sterile water and stored in a 0.5% disinfectant solution of chlorohexidine diacetate (Nolvasan®). Transmitters were rinsed again 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 cold sterilization solution for 20 min at 25°C, 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 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 5-10 mm posterior and slightly caudal to the pelvic girdle. After depressing the needle though 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 posteriorly 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 10 g or greater were tagged to ensure the transmitter weight did not exceed 5% of the individual’s body weight (Adams et al. 1998a, Brown et al. 1999). Transmitters represented between 0.41 and 4.7 % of the body weight of coho salmon smolts used in the study. Coho salmon smolts radio tagged each day were held in a net pen (1.2 x 0.61 x 0.61 m) on site for up to 7 h before being released after dark.

Release groups

One hundred seventy-six coho salmon smolts were surgically implanted with coded radio transmitters over a 13-week study period beginning 9 March and ending 2 June, 2005. Because flow releases from IGD during the study period were not predictable, and because obtaining large numbers of fish at one time was highly unlikely, we attempted to tag small replicate release groups of wild fish to extend the study over the course of the migration period. This approach was developed to increase the likelihood of measuring coho salmon smolt movement and survival in response to unpredictable changes in flows. Our goal was to tag groups of 18 wild fish from the Bogus Creek site each week and monitor their downstream movement using fixed receiver stations and manual tracking methods. Bogus Creek was the preferred capture site because it is the uppermost tributary inhabited by coho salmon within the Klamath River. As such, coho salmon smolts emigrating from Bogus Creek are most affected by IGD flow releases. Wild coho salmon smolts collected at the Shasta River trap site were used to augment weekly release groups when sufficient numbers of fish from the Bogus Creek site were not obtained. Fish collected at the Shasta River were held on site in a 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 tagged and released. On 18 April and 20 April, 30 wild fish from the Shasta River and 26 hatchery fish were tagged and released at the confluence of the Shasta River to compare emigration and habitat use between the two groups. Additionally, hatchery fish were used over the last 30 d of the study when it became apparent that sufficient numbers of wild fish would not likely be obtained to develop preliminary estimates of detection probability from the fixed station arrays (Table 1).

Table 1. Weekly number of radio transmitters implanted in wild (Bogus and Shasta creeks) and hatchery (IGH) coho salmon smolts for each collection location in 2005.

Week	6-12 Mar	13-19 Mar	20-26 Mar	27 Mar-2 Apr	3-9 Apr	10-16 Apr	17-23 Apr	24-30 Apr	1-7 May	8-14 May	29 May-4 Jun
Bogus	1	1	2	3	1		2	3	1		
Shasta			2	1	6	5	41	10	1		
IGH							26		30	20	20
Totals	1[†]	1[†]	4[†]	4[†]	7[†]	5[†]	69	13[†]	32[†]	20[†]	20[†]

[†] Indicates weeks where we were unable to implant the intended number of transmitters in wild coho salmon smolts because insufficient numbers were collected at trap locations.

Automated radio telemetry arrays

System configuration and monitoring.

Seven automated radio telemetry stations were established along the mainstem Klamath River from IGD to the estuary (Figure 1). Each station consisted of a single four-element Yagi aerial antenna mounted on a 4 m mast connected to a data-logging receiver. The specific location, rkm, receiver model and serial number, periods of operation, and operator of each array were recorded (Table 2). Stations were located at private residences or other facilities to reduce the risk of vandalism and to provide a 110 volt power supply. A backup power source was created for each unit by connecting a deep cycle 12 volt battery to a trickle charger between the 110 volt outlet and the receiver. 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 receivers was set near 75%. To ensure complete signal reception, receivers monitored each frequency for 9 s before cycling to the next frequency. This produced a continuous 36-s scan cycle. When a signal was detected, transmitter channel (frequency), code, signal strength, time, and date were logged. While in operation, stations collected data continuously (Table 2). Radio telemetry data were downloaded at each site to a portable laptop computer weekly.

Table 2. Summary of automated radio telemetry array deployment in 2005.

Site location / flow reach	rkm	Receiver type	Operator	Dates of operation
Trees of Heaven / IGD to Scott R.	280.4	Lotek SRX-400	USFWS	5/3-5/5; 5/12-7/20
Beaver Creek / IGD to Scott R.	263.5	Lotek SRX-400	USFWS	3/17-7/20
Seiad / Scott R. to Salmon R.	213.5	Lotek SRX-400	Karuk Tribe	4/13-7/11
Happy Camp / Scott R. to Salmon R.	176.8	Lotek SRX-400	Karuk Tribe	4/8-7/11
Orleans / Scott R. to Salmon R.	96.6	Orion	Karuk Tribe	3/25-7/11
Trinity Confluence/Salmon R. to Trinity R.	69.0	Lotek SRX-400	Yurok Tribe	4/22-5/4; 5/6-7/14
Highway 101 / Trinity River-Estuary	6.4	Lotek SRX-400	Yurok Tribe	4/20-4/28; 5/13-5/23; 6/2-7/13

Converting radio signals into detection histories

Radio telemetry data from automated receiver arrays were converted into detection histories to calculate detection probabilities specific to each array; a prerequisite for estimating sample size requirements for more formal survival studies. The seven automated arrays recorded 24,181 radio signals that were processed to provide reliable detection histories before calculating detection probabilities for each station. 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 coho salmon smolts from false detections. This was important because false-positive detections erroneously increase detection probability estimates of automated stations, thereby reducing the estimated number of fish needed to attain acceptable levels of precision for survival estimates for future studies. It was equally important to identify and remove false detections from the database because automated array data were used to calculate the rate of coho smolt emigration through different flow reaches over the course of the study.

Valid detections were identified by filtering radio signal data using multiple criteria (Figure 3). Data were sorted and filtered through the first four criteria using Microsoft Access. This was followed by filtering with geographic and temporal criteria, first automatically using the automated station data in Microsoft Access, then by manually cross referencing each detection event with the mobile tracking database. The resulting database output was then used to derive the downstream detection histories of fish needed to calculate detection probabilities for each array and sample size requirements for future studies (Table 3).

Mobile tracking

The reach of the Klamath River extending from the mouth of the Trinity River upstream to the confluence of the Scott River was surveyed by vehicle at least once per week to determine downstream movement of radio-tagged fish through different flow reaches of the mainstem Klamath River and to validate data obtained from automated radio telemetry arrays (Objectives 1 and 2). Accuracy of recorded fish locations made during vehicle surveys varied (< 1 m to > 0.1 km) 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. Accuracy of the recorded position in cases where fish could be approached directly was generally < 5 m and was limited by the positional accuracy of handheld global positioning system (GPS) receivers, distance of the fish from shore, and water depth.

The reach from IGD to the Scott River (rkm 309 to 234) was divided into three 25 km reaches that were surveyed weekly from a 5 m cataraft between 9 March to 10 June, 2005 to determine movement and habitat use of radio-tagged fish (Objectives 2 and 3). Data gathered during float surveys were also used to validate fixed station receiver data within the upper study flow reach (Objective 1). Accuracy of fish locations recorded during float surveys ranged from < 1 m to more than several meters depending on water depth, velocity, and activity level of the fish.

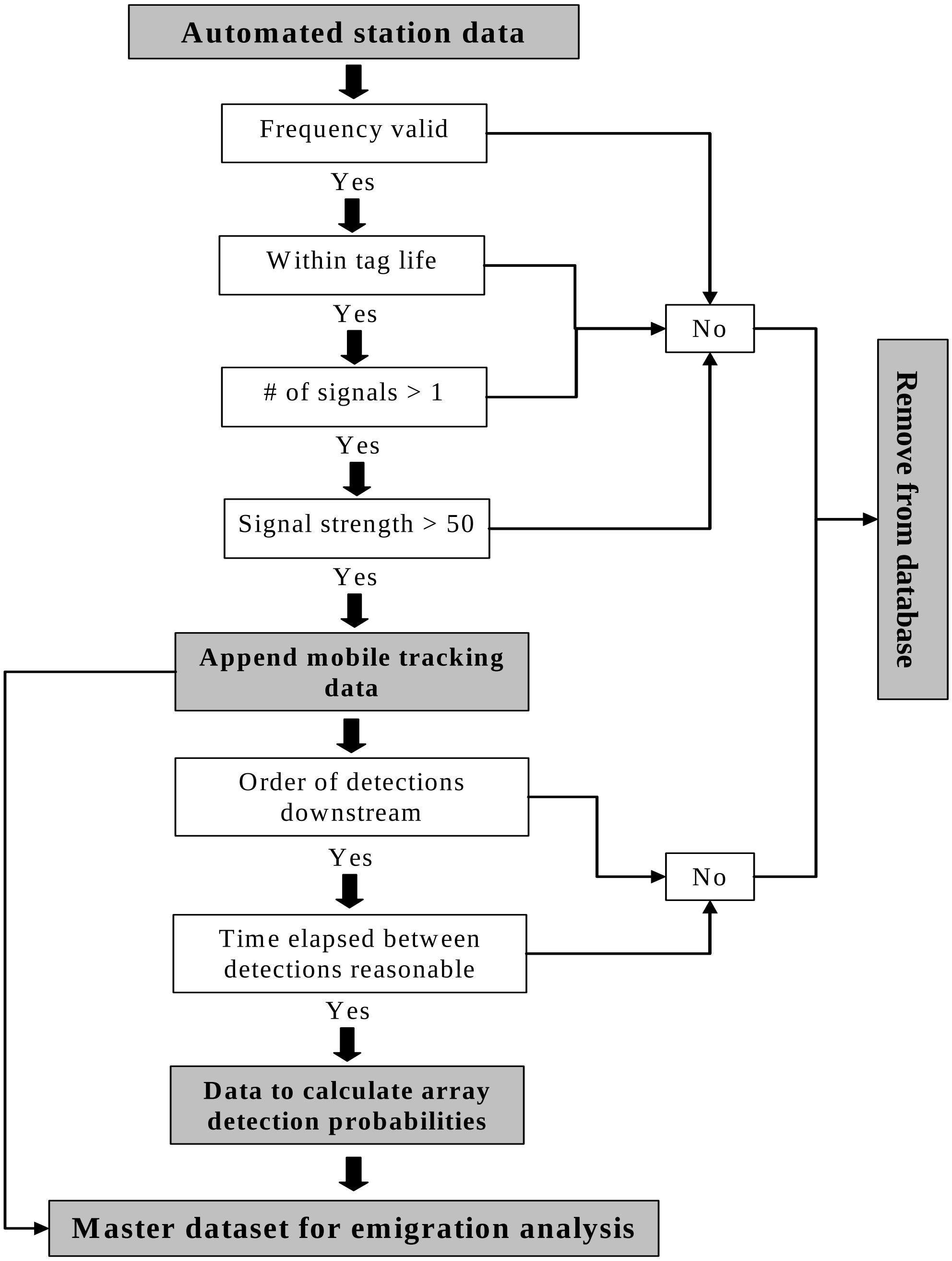

Figure 3. Data filter criteria used to identify valid radio signals recorded at seven automated radio telemetry stations, and overview of database management methods.

Table 3. Detection histories and counts of radio-tagged coho salmon smolts released during spring 2005

Release	Detection history[a]	Counts
R_1 = 176	0000100	1
	0001000	1
	0100000	14
	0110000	2
	0110100	2
	0110110	6
	0110111	3
	0111000	6
	0111100	1
	0111110	14
	0111111	6
	1000000	7
	1100000	11
	1110000	6
	1110010	1
	1110100	2
	1110101	2
	1110110	8
	1110111	5
	1111000	5
	1111010	1
	1111110	7
	1111111	8

[a] Detection history recorded at Trees of Heaven, Beaver Creek, Seiad, Happy Camp, Orleans, Trinity Confluence, and Highway 101 bridge, respectively: 1 = detected; 0 = not detected.

Radio-tagged fish were located by field crews using Lotek SRX-400 receivers equipped with Yagi antennas from 2 March to 17 June, 2005. All surveys were conducted during daylight hours. When radio-tagged fish were located, a GPS instrument was used to georeference the location as Universal Transverse Mercator (UTM) coordinates. Fish positions were then converted into rkm from aerial photographs of the river and recorded along with date, time, and a general description of the area.

Because radio telemetry detections of fish in the mainstem river below the confluence of the Trinity River relied solely on the automated station located at the Highway 101 bridge, jet boat surveys were conducted in the lower river from the estuary upriver to Coon Creek (rkm 57.5) six times from 10 May to 17 June, 2005 when the automated radio telemetry station at the Highway 101 bridge was intermittently offline.

Habitat use

River kilometer and meso-habitat type (MHT = pool, low slope, moderate slope, or steep slope) were recoded for each radio-tagged fish detected during float surveys. The MHT assigned to a fish's location was based on descriptions provided in Hardy et al. (*In preparation*). We then attempted to pinpoint the location of each fish and verify survival by observing movement over several minutes or by initiating a flight response with the raft or by wading. Although subjective to a degree, we considered the tag was in a live coho salmon smolt if upstream, downstream or across channel movement was observed during prolonged observation. When depth and underwater visibility allowed, we verified whether the tag was in a live coho salmon through underwater observation. When we were able to determine a fish's location to < 2 m and verify movement of the tag, we recorded habitat use adapted from Hardy et al. (*In preparation*; Table 4).

River conditions

Mean daily discharge (ft^3/s) for the mainstem Klamath River and selected tributaries were obtained from flow gauges operated by the U. S. Geological Survey. Water temperature was recorded hourly for the upper river using Onset temperature data loggers located directly above the Shasta (rkm 288.5) and Scott Rivers (rkm 234.0). Photoperiod was calculated as hours of daylight between sunrise and sunset using civil twilight times for Yreka, California obtained from the U.S. Naval Observatory Almanac.

Analyses

Sample size determination for survival studies

Proofed data records from detections of tagged fish at automated radio telemetry stations were used to make preliminary estimates of sample size requirements for future survival studies. Sample size estimation was based on the probability of detection at each array (capture probability) and the survival of animals from one capture period to the next. The purpose of study in 2005 was not to estimate survival per se as some critical

Table 4. Habitat use criteria recorded for radio-tagged coho salmon during 2005 float surveys.

- Channel configuration (main-channel, side-channel, split-channel)
- Location in channel (mid-channel or edge)
- Meso-habitat type (pool, low slope, moderate slope, steep slope)
- Fish distance from shore
- Fish distance to shear
- Stream margin edge type (SMET)
- Substrate (dominant / subdominant)
- Cover code
  - In-water overhead
  - Out of water overhead
  - Object cover type
- Mid column water velocity
- Water column depth at fish

assumptions of survival estimation may have been violated (Burnham et al. 1987). Thus, while useful for the purpose of estimating sample sizes for future studies of survival, the survival estimates generated as part of the sample size determination analysis are provisional and not presented in this report.

Estimates of precision of survival estimates were generated over a range of sample sizes. The "Survival Under Proportional Hazards" program was used to generate provisional Cormack-Jolly-Seber survival estimates between detection arrays (Lady et al. 2001). Provisional survival estimates from this process were used with capture probabilities calculated beginning when each array was placed in operation (Table 3). Capture probabilities were calculated in this manner to mimic methods proposed for use in subsequent studies, assuming all arrays would be installed prior to fish releases. Dates the arrays were offline between their start date and final end date in 2005 were not removed from the analysis. These data were then processed using the program Sample Size 1.3 (Lady et al. 2003) to estimate 95% confidence intervals of hypothetical survival estimates based on the single-release-recapture survival model from hypothetical releases of 10 to 1,000 fish upstream of the first detection array.

Migratory characteristics of wild and hatchery coho salmon smolts

We measured the downstream migration rates of wild and hatchery juvenile coho salmon through four index reaches. Tributaries with accretions that regularly contributed 20% or more relative to the mainstem river flow were used as geographic boundaries to delineate four different index reaches for study within the mainstem river. Index reaches were from IGD to Scott River, Scott River to Salmon River, Salmon River to Trinity River, and Trinity River to the Klamath Estuary (Figure 1). First and last positions (rkm) of radio-tagged fish from all survey methods (car, boats, automated radio telemetry arrays) were used to determine the migration rate (km/d) of fish within an index reach at 7-d intervals over the entire study period. Initially, we examined the influence of 20 different time intervals (1, 2, 3,…20-d) on the number of individual migration rate estimates (N) for each fish type (wild and hatchery) produced for each index flow reach. The 7-d time interval was selected because it produced the largest sample size for each of the four index reaches while minimizing variability of flow, day length, and temperature conditions experienced by tagged fish within intervals.

We evaluated the effects of river flow, day length, water temperature, fish length, and release date (independent or predictor variables) on the migration rate (dependent variable) of wild and hatchery juvenile coho salmon using bivariate and multivariate least-squares regression analyses. Because we lacked a direct physiological measurement of smoltification for individual fish (e.g. gill ATPase) we considered day length, water temperature, fish length, and release date as surrogates for overall smoltification status (Berggren and Filardo 1993, Giorgi et al. 1997). To calculate flow, day length, and temperature conditions encountered by migrating smolts within an index reach, we calculated the mean value for each variable for the 7-d interval. Mean daily flows and water temperatures were used to calculate 7-d averages. Average 7-d flows for a reach were calculated as the mean of flow estimates for the upstream and downstream ends of each index reach over that 7-d period. During the study period, temperature data were only available for the upper index reach (IGD to Scott River). Mean 7-d temperatures within this reach were calculated as the daily average of measurements taken directly upstream of the Scott and Shasta Rivers for the specific 7-d time interval.

Prior to conducting bivariate and multivariate analyses, we explored the potential of using hatchery fish as surrogates for wild fish by examining the migration rates of groups of wild and hatchery fish released from the Shasta River trap site on 18 and 20 April, 2005, respectively. The non-parametric Mann-Whitney procedure was used to test for significant differences ($\alpha = 0.05$) in the migration rate of fish in each group because the underlying assumptions of homogeny of variance and normality necessary for reliable application of parametric procedures could not be met after log*e*-transforming migration rate estimates (Sokal and Rohlf 1995). Analyses were performed for each index reach separately, and for all four reaches combined by pooling the data.

Before we examined bivariate and multivariate models, we examined all data for variance and linearity. Residual plots from bivariate analysis were used to examine the linearity and variance of untransformed and $\log_e$-transformed variables. In all cases $\log_e$ transformation improved linearity and variance patterns of the dependent variable.

Bivariate least-squares linear regression was used to describe the relationship between migration rates of wild and hatchery coho salmon smolts within an index reach and each independent variable separately. Before conducting multivariate analysis, we calculated Pearson correlation matrices to test for multicollinearity among independent variables. If two independent variables were correlated ($P \leq 0.05$ and $r^2 \geq 0.70$), we removed the variable that had the weakest relationship (lowest r^2) with migration rate. Stepwise multiple regression was then used to describe relationships between migration rate and the final subset of independent variables for wild and hatchery coho salmon smolts within each index reach.

Mainstem rearing

Fish behavior was identified as "rearing" within the mainstem Klamath River if a tag was determined to be in a live fish as previously described, and resided at a specific location for more than 24 h. We classified rearing behavior into two categories based on the level of certainty that could be applied to each observation. The first category, category 1, included fish that remained at a specific location for more than 24 h, and then resumed their downstream migration. The second category, category 2, was comprised of fish that migrated to and remained at a specific location until radio contact was lost. We report observations in this second category as rearing, even though in some cases we were not able to visually confirm that the tag was still in a live coho salmon. While steps were taken to assess tag movement to determine if these observations were associated with live fish, we were unable to rule out the possibility that these tags may have been in the stomachs of predatory fish. Therefore, the certainty of coho salmon smolts exhibiting rearing behavior is less for category 2 observations than for category 1 observations. For both categories of rearing, we calculated distance traveled (km) before rearing, total time (d) and proportion time at liberty spent rearing.

RESULTS

River conditions

Mean daily discharge (ft^3/s) of the four study flow reaches differed significantly (ANOVA; $F_{0.05\ (1)\ 3,\ 608} = 193.40$; $P < 0.000$) during the study period (Figure 4). The mean (range) water temperature measured upstream of the Shasta and Scott Rivers during the study period were 13.1 ºC (8.5-18.0) and 13.4 ºC (8.9-18.4). Water temperatures increased with day length on the upper index reach where measurements were made (IGD to Scott River). Water temperatures at the two locations did not differ significantly ($t_{0.05\ (2),\ 28} = 2.048$, $P = 0.80$) during the study period and were highly correlated ($r = 0.99$).

Sample size determination

Capture probabilities of radio-tagged coho smolts from 2005 were high at all but one automated radio telemetry station (Table 5). The low capture probability estimate for the Happy Camp station was likely caused by the low gain level setting of the receiver (50%) required due to local interference around the same frequency bandwidth at this site.

The predicted sample size required for estimating survival for future studies was dependent largely on the desired precision of the estimate and the length of the reach survival was estimated through. The precision of the hypothetical survival estimates decreased with distance from the release site due to attrition of tagged fish as they moved downstream. For example, at any given sample size, the precision of the estimate from

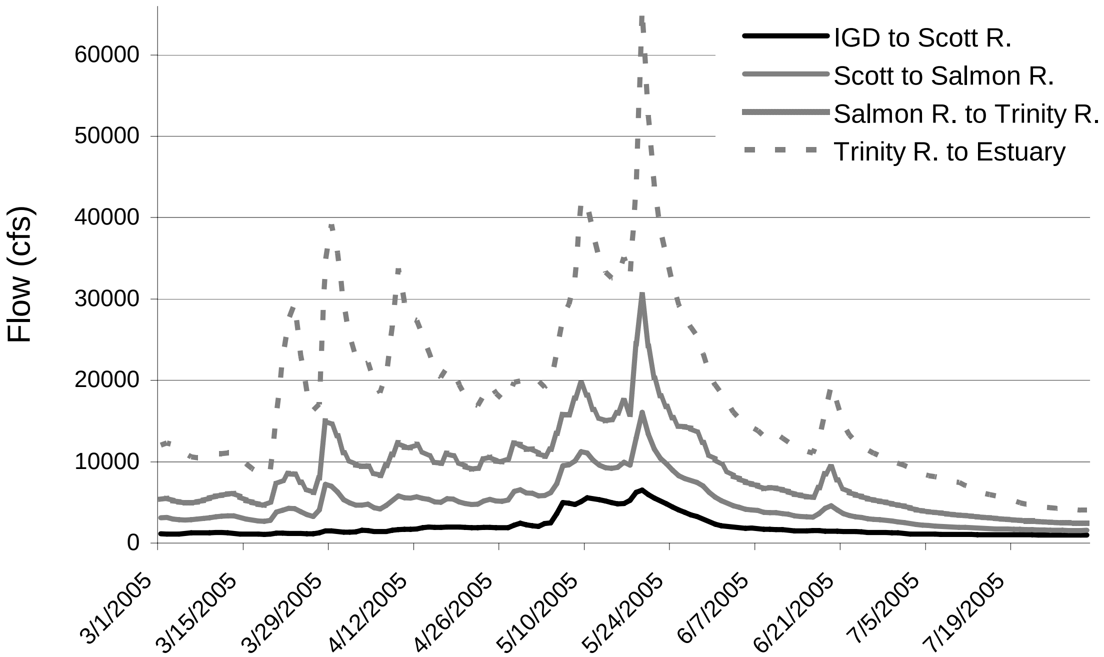

Figure 4. Mean daily river discharge (f^3/s) of the four index reaches during the 2005 study period.

Table 5. Capture probabilities (*P*) and standard error (SE) of each automated telemetry array used in 2005 from the date of operation to the end of the study. P was calculated as r/(z + r), where r is the number of tagged fish detected at the site that were also detected downstream and z is the number of fish not detected at the site that were detected downstream of the site.

Site Location	*P*	SE	r	z
Trees of Heaven	0.84	0.05	41	8
Beaver Creek	0.98	0.02	85	2
Seiad	0.99	0.01	75	1
Happy Camp	0.55	0.06	36	29
Orleans	0.97	0.02	59	2
Trinity Confluence	0.87	0.09	13	2
Highway 101[a]	na	na	na	na

[a] The capture probability of the last array (Hwy 101) cannot be calculated as there were no sites downstream to derive z and r.

release to the Trees of Heaven site is smaller than from the release site to Beaver Creek and so on with increased distance from the release site (Figure 5). Precision was improved greatly with increased sample size up to about 200, but subsequent improvement diminished as sample size was increased beyond 200. The predicted confidence interval around a survival estimate from release to the confluence of the Klamath and Trinity rivers (confluence; the most downstream site to which provisional survival could be calculated in 2005) was ± 10.5% at N = 200 and ± 4.7% at N = 1,000.

We estimate that approximately 200 tagged fish of hatchery origin and 200 naturally-produced fish would be sufficient to produce a system-wide survival estimate with 95% confidence intervals of ± 10% or less for each group using a Single Release Recapture Model (Figure 5). Estimated precision using a paired-release design and the release-recapture model for the IGD to Shasta River reach is 15% at a sample size of 100 treatment + 100 control = 200 total tagged fish. This is about three times larger than the expected precision estimated for the same reach using the single-release (known fate) model. If the assumptions associated with a known fate model can be met, its use will result in greater precision for a given sample size than for estimates generated using a paired-release design.

Fish size

The mean fork length (FL mm) and weight (g) of all wild and hatchery coho salmon smolts tagged during the study did not differ significantly ($t_{0.05\,(2),\,174} = 1.59$, $P = 0.113$, Power = 0.38), and ($t_{0.05\,(2),\,174} = 1.14$, $P = 0.257$, Power = 0.21), respectively (Table 6). Similarly, the 30 wild and 26 hatchery fish released at the Shasta River trap site (18-20 April) to directly compare migration rate between wild and hatchery fish did not differ significantly in terms of mean FL ($t_{0.05\,(2),\,54} = 1.87$, $P = 0.06$. Power = 0.48) or mean weight ($t_{0.05\,(2),\,54} = 1.95$, $P = 0.06$. Power = 0.52).

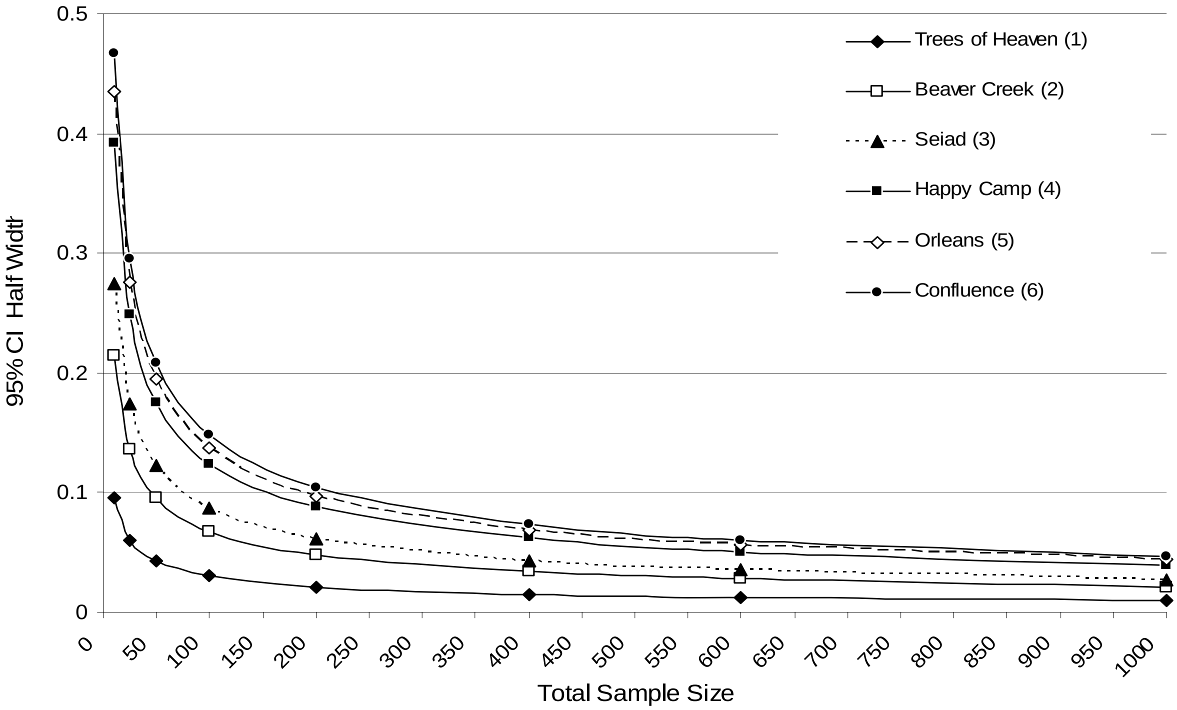

Figure 5. The predicted relation between sample size and precision of theoretical survival estimates using Single Release Recapture Model based on data collected in 2005. Numbers following detection array names indicate their order from the uppermost to the lowermost along the Klamath River downstream from Iron Gate Dam.

Table 6. Descriptive statistics for wild and hatchery coho salmon smolts radio tagged at Bogus Creek, Shasta River, and Iron Gate Hatchery during 2005

	Wild coho (*N* = 80)		Hatchery coho (*N* = 96)	
	Fork length (mm)	Weight (g)	Fork length (mm)	Weight (g)
Mean	143.9	32.34	145.5	31.94
SD	21.0	15.40	15.6	10.78
Range	101-223	10.4 – 123.6	115 - 213	12.5 - 85.1

Migration rates of wild and hatchery groups released at Shasta River 18-20 April

Slightly more than 93% of wild fish from the 18-20 April release were detected downstream after tagging (Table 7), producing a total of 108 estimates of migration rate for individual fish (Table 8). Approximately 88% of hatchery fish were detected after tagging, generating 55 migration rate observations. The decline in detections of radio-tagged coho salmon smolts along the longitudinal river gradient was less among wild fish compared to hatchery fish, especially in the lower reaches (Table 7). This created imbalance in the sample size among comparison groups below the first index reach, making it difficult to accurately determine if differences existed in migration rates for reaches two through four. Analysis revealed wild fish from the paired release migrated through reach one significantly faster than hatchery fish released 48 h later (Table 8). However, analysis of the average of the median migration rate values of individual fish through the four flow reaches indicated that the migration rates of wild and hatchery fish were similar across all flow reaches. Discharge from IGD was similar over this 48-h period, dropping from 1,979 ft^3/s on 18 April to 1,938 ft^3/s on 20 April.

Table 7. Numbers of radio-tagged smolts released at the Shasta River trap site from 18-20 April, 2005 and later detected within the four index flow reaches

Tag group	Number (%) detected reach 1	Number (%) detected reach 2	Number (%) detected reach 3	Number (%) detected reach 4	Total number (%) detected
Wild (N=30)	28 (93.3)	17 (56.7)	13 (43.3)	7 (23.3)	29 (96.7)
Hatchery (N=26)	23 (88.5)	4 (15.4)	2 (7.7)	1 (3.8)	23 (88.5)

Table 8. Number and median (ranges in parentheses) value of migration rate (km/d) estimates for wild and hatchery coho salmon smolts released at the Shasta River trap site 18-20 April, 2005.

Fish type	Reach	*N*	Median migration rate	P-value
Wild	1	64	1.42 (-0.14 – 105.38)	0.01[a]
Hatchery	1	47	0.06 (-3.63 – 27.10)	
Wild	2	23	13.58 (0.00 – 147.00)	[c]
Hatchery	2	5	30.74 (0.00 – 44.82)	
Wild	3	13	47.60 (15.10 – 184.0)	[c]
Hatchery	3	2	23.40 (2.20 – 44.50)	
Wild	4	8	24.31 (0.00 – 47.79)	[c]
Hatchery	4	1	39.87	
Wild	1-4 combined	108	21.73[b] (-0.14 – 184.00)	
Hatchery	1-4 combined	55	23.51[b] (-3.63 – 44.82)	

[a] significant difference in the median emigration rate (Mann-Whitney test ; 2-tailed; α = 0.05)
[b] values represent the average of median migration rate values in each reach.
[c] statistical analysis not performed because of low / imbalanced number of observations.

Migratory behavior of wild coho salmon smolts

The mean fork lengths (SD) of the subset of radio-tagged wild coho salmon detected at the last automated radio telemetry array (rkm 6.4) was 150.2 mm (± 20.5) and did not differ significantly from the size of all wild fish at release (142.8 mm (± 17.4); $t_{0.05\,(2),\,88} = 1.29$; $P = 0.201$; Power = 0.78). This suggests the size of wild fish at the time of release did not influence the likelihood of being detected above the estuary. Measurements of the subset of fish detected at rkm 6.4 represent the size of fish at time of release, not as they migrated past the last radio telemetry array.

Wild coho salmon index reach 1 (IGD to Scott River)

Seventy four (93%) of the 80 radio-tagged wild coho salmon released were detected within index reach 1 during the 2005 study period. From these detections we were able to calculate 151 migration rate estimates. The median migration rate of wild coho salmon in this reach was 0.26 km/d (range = -0.62–141.25 km/d). Mean 7-d flows, day lengths, and river temperatures experienced by wild coho salmon migrating through reach 1 during the study period ranged from 1,147 to 5,244 ft^3/s, 13.8 to 17.2 h, and 9.3 to 14.9ºC, respectively (Table 9).

Table 9. Number of migration rate estimates, median migration rates (km/d) of radio-tagged coho salmon smolts released in 2005, and range of indices (flow, day length, temperature, fish length, and release date) for index reaches used in bivariate and multivariate analysis.

Fish type (sample size)	Reach	Radio-tagged smolts			Range of indices for detected fish			
		Migration rate scores (*n*)	Median migration rate (km/d)	Flow (ft^3/s)	Day length (h)	Water temperature (ºC)	Fork length (mm)	Release date (day of year)
Wild (n=80)	1	151	0.26	1,147-5,244	13.8-17.2	9.3-14.9	102-223	68-123
	2	47	21.90	5,109-11,211	15.9-17.2	na	113-179	95-123
	3	37	43.80	9,964-19,957	15.2-17.4	na	113-179	95-123
	4	11	39.90	33,549-42,379	16.6-17.2	na	113-172	108-123
Hatchery (n=96)	1	131	3.14	1,584-5,244	15.9-17.7	12.7-17.8	115-181	110-153
	2	29	38.50	3,490-11,211	16.2-17.7	na	124-175	124-175
	3	24	78.90	6,304-19,957	16.9-17.7	na	119-175	110-175
	4	13	39.90	24,464-35,029	16.9-17.7	na	124-164	110-153

Mean flow, which correlated significantly ($P \leq 0.001$) and had a positive relationship with migration rate (Figure 6), was the most important variable in the bivariate analysis explaining 25% of the variation in migration rates (Table 10). Mean day length, temperature, fish length, and release date were all positively correlated with migration rate and significant in the bivariate models (Figure 6). However, these variables explained less variation in the migration rate of juvenile coho salmon than did flow (Table 10). The multivariate model incorporating mean flow and fish length (positive relationships) explained only 1% more of the variation in migration rate than did the mean flow bivariate model (Table 11). Predictor variables day length and temperature were excluded from the model because they were strongly correlated with flow ($R^2 > 0.70$) and had lower R^2 values. Release date did not significantly improve the fit of the stepwise model (α to enter or remove ≤ 0.15).

Wild coho salmon index reach 2 (Scott River to Salmon River)

During the 2005 migration period, 41 (51%) of the 80 radio-tagged wild coho salmon were detected in reach 2, producing 47 migration rate estimates. The median migration rate of wild coho salmon in reach 2 was 21.90 km/d (range = 0.00 – 193.42 km/d). Mean 7-d flows and day lengths experienced by wild coho salmon migrating through reach 2 during the study period ranged from 5,109 to 11,211 ft^3/s, and 15.9 to 17.2 h, respectively (Table 9).

Flow was the only variable in the bivariate analysis that correlated significantly with migration rate (negative relationship; $P \leq 0.01$), and explained only 14% of the variation in migration rates (Figure 7; Table 10). We could not develop a multivariate model that included day length because day length correlated strongly with flow ($R^2 = 0.92$). Using mean flow, fish length and release date as the starting predictor variables, only flow entered the multivariate model, explaining the same amount of variation in migration rates as the bivariate analysis (Table 11).

Wild coho salmon index reach 3 (Salmon River to Trinity River)

During the 2005 migration period, 37 (46%) of the 80 radio-tagged wild coho salmon were detected in reach 3. Detection of these fish produced 37 migration rate estimates. The median migration rate of wild coho salmon in reach 3 was 43.8 km/d (range = 0.00 – 212.3 km/d). Mean 7-d flows and day lengths experienced by wild coho salmon migrating through reach 3 during the study period ranged from 9,964 to 19,957 ft^3/s, and 15.2 to 17.4 h, respectively (Table 9).

Release date was the only predictor variable significantly correlated (positive relationship, $P \leq 0.01$) with migration rate in any of the bivariate analysis (Figure 8) and it explained 27% of the variation in migration rates. With all predictor variables included in the starting multivariate model, release date was the only variable to enter the model and explained the same amount of variation in migration rate as the bivariate analysis ($R^2 = 0.27$; Table 11)

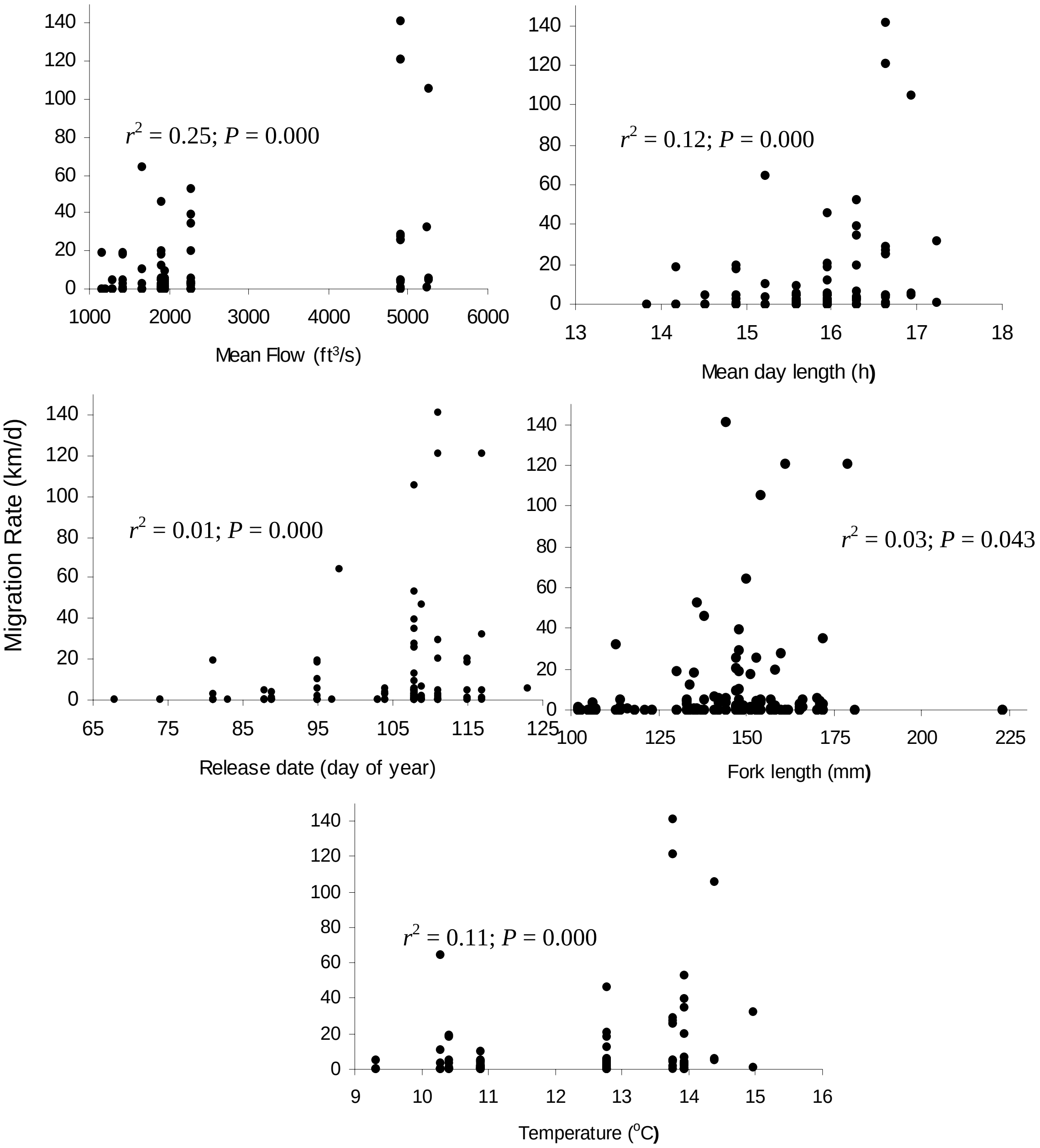

Figure 6. Relationships between migration rates of wild juvenile coho salmon within index reach 1 and independent variables during 2005. Solid circles represent non-transformed observed migration rates; r^2 and P-values are from bivariate analysis of $\log_e$-transformed values of migration rate.

Table 10. Bivariate least-squares regression model results of migration rates (dependent variable) of wild coho salmon (N = 80) radio tagged at Bogus Creek and Shasta River through four index study reaches during spring, 2005. All analysis were performed after $\log_e$-transformation of dependent variable.

Reach	Independent variable	Regression coefficients	SE	*t-value* (β = 0)	Probability (β = 0)	*r2*
1	Constant	-0.3932	0.2146	-1.83	0.069	0.25
	Flow	0.000616	0.000088	6.98	0.000	
	Constant	-10.001	2.344	-4.27	0.000	0.12
	Day length	0.6973	0.1490	4.68	0.000	
	Constant	-2.6499	0.8420	-3.15	0.002	0.11
	Temperature	0.3004	0.06905	4.35	0.000	
	Constant	-0.4407	0.6952	-0.63	0.527	0.03
	FL	0.00977	0.004793	2.04	0.043	
	Constant	-2.6175	0.9084	-2.88	0.005	0.10
	Release date	0.035	0.00883	3.96	0.000	
2	Constant	5.0684	0.7815	6.49	0.000	0.14
	Flow	-0.00026	0.000094	-2.75	0.009	
	Constant	22.17	10.33	2.15	0.037	0.07
	Day length	-1.1611	0.6254	-1.86	0.070	
	Constant	5.616	2.048	2.74	0.009	0.04
	FL	-0.0177	0.0137	-1.29	0.204	
	Constant	5.510	4.346	1.27	0.211	0.01
	Release date	0.02309	0.0397	-0.58	0.564	
3	Constant	2.527	1.318	1.92	0.063	0.02
	Flow	0.000071	0.000085	0.84	0.406	
	Constant	-14.341	9.561	-1.50	0.143	0.09
	Day length	1.0775	0.5735	1.88	0.069	
	Constant	5.098	2.901	1.76	0.088	0.01
	FL	-0.01009	0.01962	-0.51	0.610	
	Constant	-10.180	3.871	-2.63	0.013	0.27
	Release date	0.1271	0.03562	3.57	0.001	
4	Constant	-2.761	1.965	-1.41	0.194	0.56
	Flow	0.00018	0.000054	3.41	0.008	
	Constant	-46.07	13.48	-3.42	0.008	0.60
	Day length	2.9564	0.7972	3.71	0.005	
	Constant	9.294	1.267	7.30	0.000	0.66
	FL	-0.0369	0.0085	-4.24	0.002	
	Constant	-7.775	4.829	-1.61	0.142	0.40
	Release date	0.1052	0.04343	2.42	0.038	

Table 11. Stepwise multivariate regression model results of migration rates (dependent variable) of wild coho salmon (N = 80) radio tagged at Bogus Creek and Shasta River through four index study reaches during spring, 2005. All analysis performed after $\log_e$-transformation of dependent variable; α to enter = 0.15.

Reach	Independent variable	Regression coefficients	t-value (β = 0)	Probability (β = 0)	R^2
1	Constant	-1.439			0.26
	Flow	0.00060	6.80	0.000	
	FL	0.0073	1.59	0.115	
2	Constant	5.068			0.14
	Flow	-0.00026	-2.75	0.009	
3	Constant	-10.18			0.27
	Release date	0.127	3.57	0.001	
4	Constant	-23.745			0.84
	Fish length	-0.0251	-3.47	0.008	
	Day length	1.86	2.99	0.017	

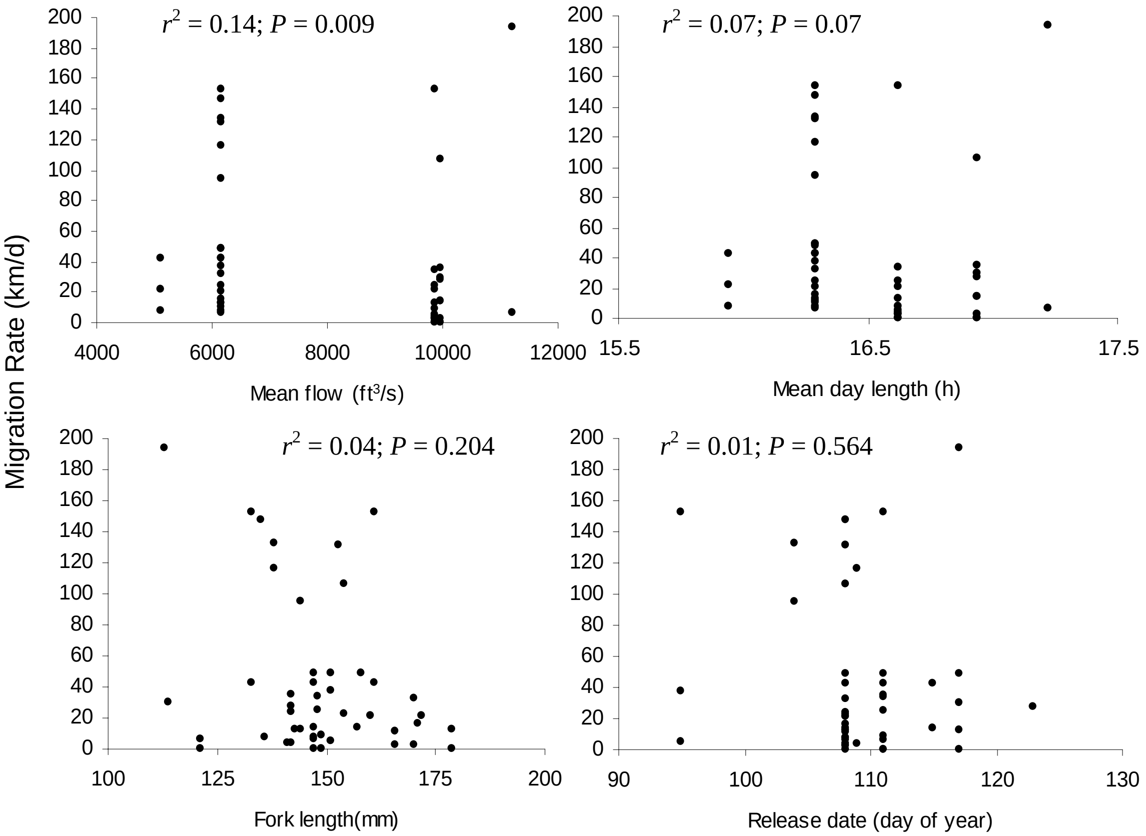

Figure 7. Relationships between migration rates of wild juvenile coho salmon within index reach 2 and independent variables during 2005. Solid circles represent non-transformed observed migration rates; r^2 and P-values are from bivariate analysis of $\log_e$-transformed values of migration rate.

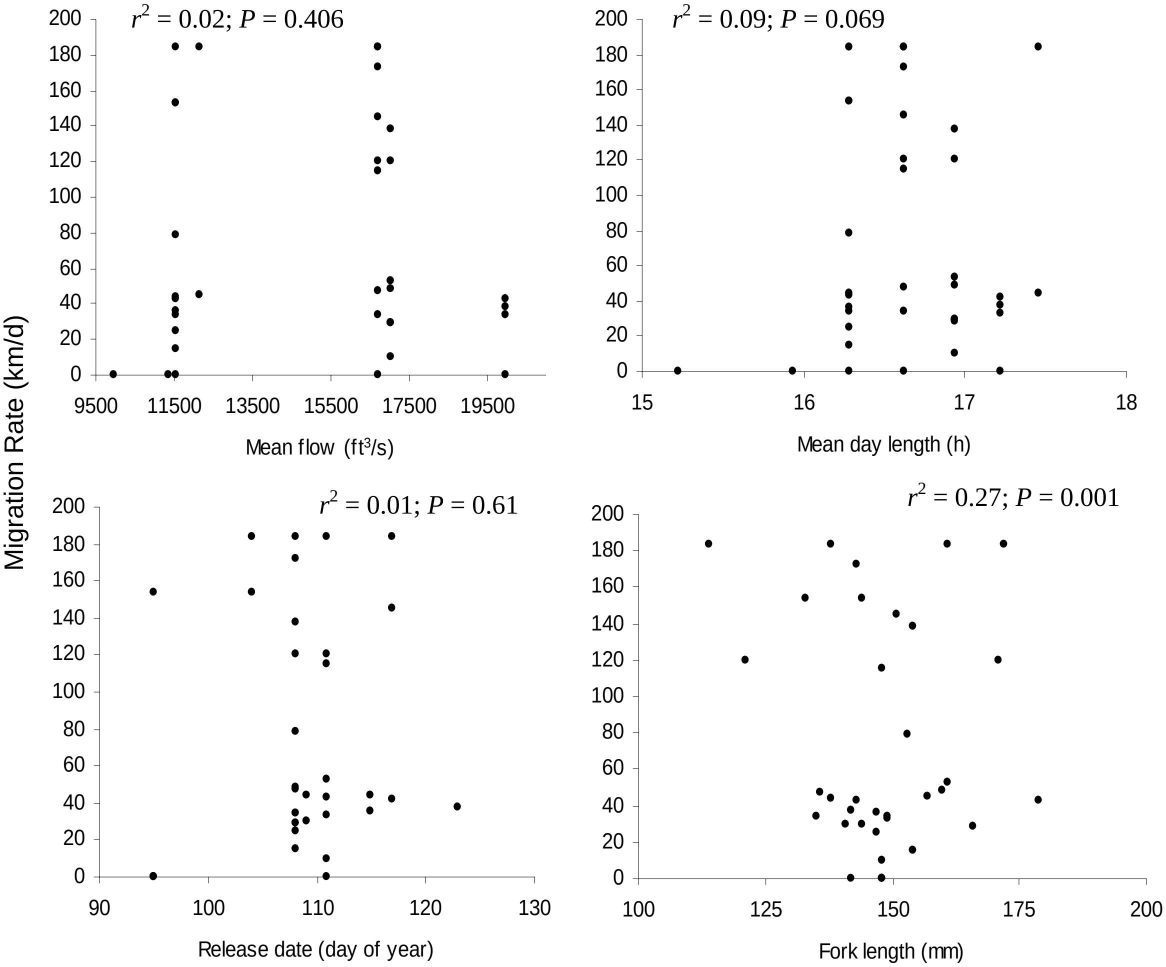

Figure 8. Relationships between migration rates of wild juvenile coho salmon within index reach 3 and independent variables during 2005. Solid circles represent non-transformed observed migration rates; r^2 and P-values are from bivariate analysis of $\log_e$-transformed values of migration rate.

Wild coho salmon index reach 4 (Trinity River to Estuary)

Twelve (15%) of the 80 wild coho salmon smolts radio tagged during the 2005 migration season were detected within index reach 4, producing 12 migration rate estimates. The median migration rate of wild fish through reach 4 was 39.9 km/d (range = 21.3 – 195.6 km/d). Mean 7-d flows and day lengths experienced by these fish ranged from 33,549 to 42,379 ft^3/s, and 16.6 to 17.2 h, respectively.

All independent variables were significantly correlated with migration rate in bivariate analyses (Table 10). Fish length was inversely related with migration rate and explained the most variation (66%) in migration rates (Table 10). Day length, flow, and release date were all positively correlated with migration rate (Figure 9), and explained 60%, 56%, and 40% of the variation in migration rates (Table 10). In the multivariate model, fish length (negative correlation) and day length (positive correlation) together explained 84% of the variation in migration rate (Table 11). We were unable to develop a multivariate model that included flow and day length because the two variables were strongly correlated ($R^2 = 0.86$).

Rearing behavior of wild coho salmon smolts

Nine (11%) of the 80 wild juvenile coho salmon tagged traveled a median distance of 62.8 rkm (range 3.4 – 173.0 rkm), then resided at a specific location for at least 24 h before resuming their downstream migration (Category 1). The median number of days these fish resided at specific rearing locations was 4.5 d (range 3 – 22 d) or an average proportion of 0.36 (range 0.11 – 0.88) of their total time at liberty. Six of these 9 fish were eventually detected near the estuary after traveling an average of 219.1 rkm from their release locations.

In addition, 13 (16%) of the 80 wild coho salmon smolts tagged migrated downstream a median distance of 29.5 rkm (range 0 – 205.8 rkm) then remained at a specific location for the remainder of the tag-life (Category 2). The median number of days these tags were detected at their last location was 16.0 d (range 1 – 37 d). The proportion of the total time these tags were found at their last detection location averaged 13.5 d (range 4 – 30 d).

Migratory behavior of hatchery coho salmon smolts

The mean fork lengths (SD) of the subset of radio-tagged hatchery coho salmon detected at the last automated radio telemetry array (rkm 6.4) was 146.2 mm (± 12.1) and did not differ significantly from the size of all wild fish at release (146.8 mm (± 18.8) ($t_{0.05\,(2),\,88} = -0.12$; P = 0.905; Power = 0.06). This suggests the size of hatchery fish at the time of release did not influence the likelihood of being detected above the estuary. Measurements of the subset of fish detected at rkm 6.4 represent the size of fish at time of release, not as they migrated past the last radio telemetry array.

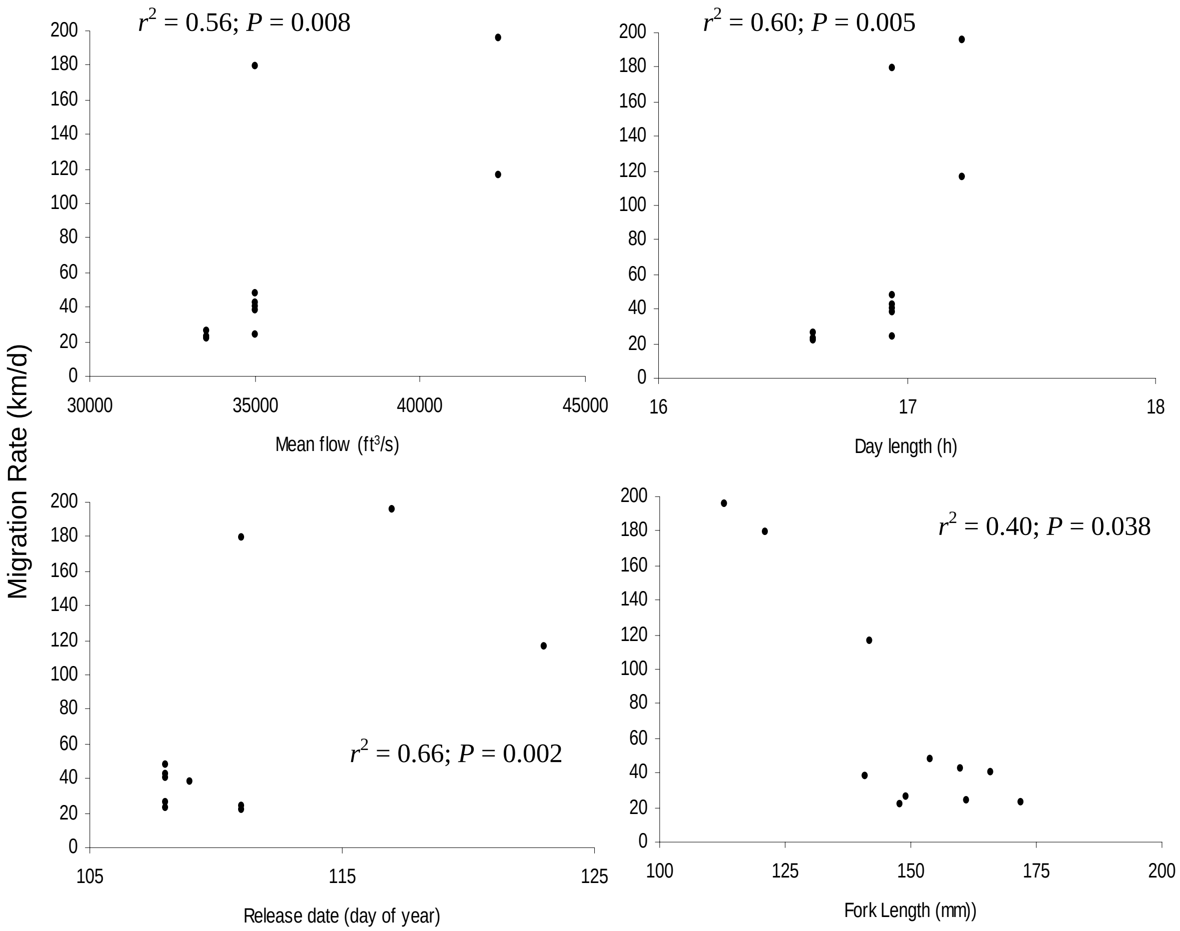

Figure 9. Relationships between migration rates of wild juvenile coho salmon within index reach 4 and independent variables during 2005. Solid circles represent non-transformed observed migration rates; r^2 and P-values are from bivariate analysis of $\log_e$-transformed values of migration rate.

Hatchery coho salmon index reach 1 (IGD to Scott River)

We detected 82 (85%) of the 96 radio-tagged hatchery coho salmon within index reach 1 during the 2005 study period. Detections of these fish produced a total of 131 migration rate estimates for the reach. The median migration rate of hatchery coho through reach 1 was 3.14 km/d (range = -3.63 – 188.33 km/d). Mean 7-d flows, day lengths, and water temperatures experienced by hatchery coho salmon migrating through reach 1 during the study period ranged from 1,584 to 5,244 ft^3/s, 15.9 to 17.7 h, and 12.7 to 17.8 ºC respectively (Table 9).

Day length, release date, water temperature, and fork length, were all significantly correlated with migration rate (positive relationship, $P< 0.01$), and explained 34, 31, 28 and 6 % of the variation in migration rates (Figure 10;Table 12). Migration rate and flow were not significantly correlated. Day length and fish length together explained slightly more (40%) of the variation in migration rate of juvenile coho salmon in reach 1 during the study period (Table 13). Flow, water temperature, and release date were excluded from the model because they were correlated with day length and lower R^2 values.

Hatchery coho salmon index reach 2 (Scott River to Salmon River)

During the 2005 migration period, 29 (30%) of the 96 radio-tagged hatchery coho salmon were detected in index reach 2, producing 29 migration rate estimates. The median migration rate of hatchery coho salmon in reach 2 was 38.5 km/d (range = 0.00 – 193.4 km/d). Mean 7-d flows and day lengths experienced by wild coho salmon migrating through reach 2 during the study period ranged from 3,490 to 11,211 ft^3/s, and 16.2 to 17.76 h (Table 9).

No predictor variable was significantly correlated with migration rate in the bivariate analysis (Figure 11; Table 12). In the multivariate analysis, flow and day length entered the model and explained 39% of the variation in migration rate (Table 13). Release date was not included in the model because it was strongly correlated with day length and had a lower R^2 value.

Hatchery coho salmon index reach 3 (Salmon River to Trinity River)

Twenty four (25%) of the 96 hatchery fish tagged were detected within index reach 3, producing a total of 23 migration rate estimates. The median migration rate of hatchery fish through this reach was 78.9 km/d (range 2.2 – 197.1 km/d). The mean 7-d flows and day lengths experienced by hatchery fish migrating through reach 3 ranged from 6,304 to 19,957 ft^3/s, and 16.0 to 17.8 h (Table 9).

None of the predictor variables were significantly correlated with the migration rate of radio-tagged hatchery coho salmon in any of the bivariate analysis (Figure 12; Table 12). In the multivariate analysis flow and release date were excluded from the model because they were correlated with day length and had lower R^2 values. Neither day length or fish length entered the multivariate model (Table 13).

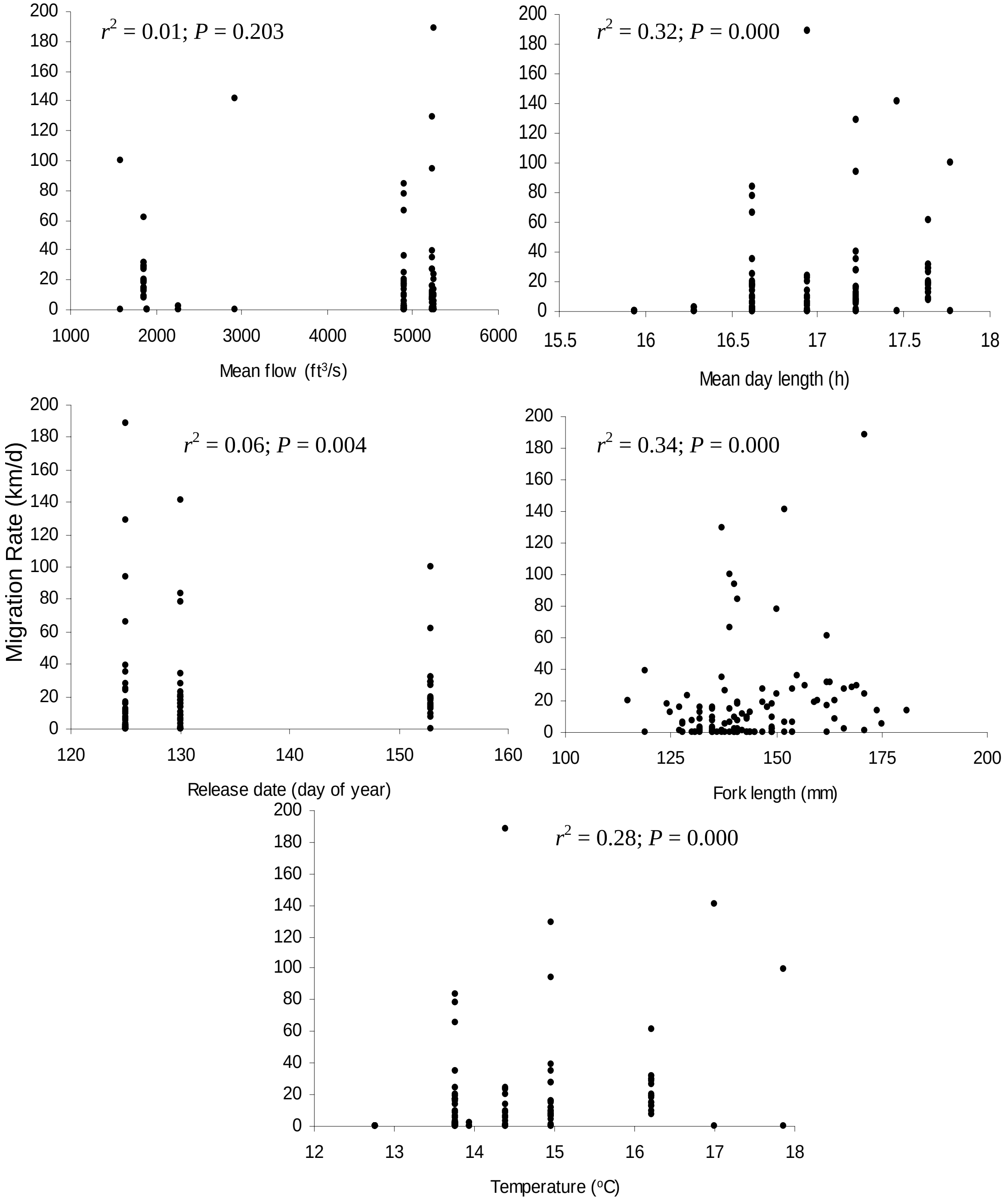

Figure 10. Relationships between migration rates of hatchery juvenile coho salmon within index reach 1 and independent variables during 2005. Solid circles represent non-transformed observed migration rates; r^2 and P-values are from bivariate analysis of $\log_e$-transformed values of migration rate.

Table 12. Bivariate least-squares regression model results of migration rates (dependent variable) of hatchery coho salmon (N = 96) radio tagged at Bogus Creek and Shasta River through four index study reaches during spring, 2005. All analysis performed after $\log_e$-transformation of dependent variable

Reach	Independent variable	Regression coefficients	SE	t-value ($\beta = 0$)	Probability ($\beta = 0$)	r^2
1	Constant	1.2143	0.3757	3.23	0.002	0.01
	Flow	0.0001127	0.00008817	1.28	0.203	
	Constant	-26.261	3.424	-7.67	0.000	0.34
	Day length	1.6588	0.2033	8.16	0.000	
	Constant	-8.383	1.416	-5.92	0.000	0.28
	Temperature	0.69885	0.09818	7.12	0.000	
	Constant	-2.666	1.487	-1.79	0.075	0.06
	FL	0.03013	0.01031	2.92	0.004	
	Constant	-5.8162	0.9814	-5.93	0.000	0.32
	Release date	0.059892	0.007809	7.67	0.000	
2	Constant	1.8109	0.8397	2.16	0.40	0.11
	Flow	0.0001767	0.00009474	1.87	0.073	
	Constant	11.09	16.40	0.68	0.504	0.01
	Day length	-0.4515	0.9471	-0.48	0.637	
	Constant	-0.157	3.232	-0.05	0.962	0.04
	FL	0.02360	0.02214	1.07	0.292	
	Constant	1.071	2.835	0.38	0.708	0.02
	Release date	0.01694	0.02164	0.78	0.440	
3	Constant	4.0290	0.5545	7.27	0.000	0.00
	Flow	0.00000084	0.0000414	0.02	0.984	
	Constant	-6.20	14.47	-0.43	0.673	0.02
	Day length	0.5866	0.8286	0.71	0.487	
	Constant	4.981	2.053	2.43	0.024	0.03
	FL	-0.00654	0.01418	-0.46	0.650	
	Constant	3.644	2.012	1.81	0.084	0.00
	Release date	0.00297	0.01503	0.20	0.845	
4	Constant	4.6432	0.8991	5.16	0.000	0.14
	Flow	-0.00006481	0.0000483	-1.34	0.207	
	Constant	-28.25	25.13	-1.12	0.285	0.13
	Day length	1.805	1.428	1.26	0.232	
	Constant	7.068	5.092	1.39	0.190	0.05
	FL	-0.02605	0.03475	-0.75	0.468	
	Constant	-3.815	2.410	-1.58	0.142	0.46
	Release date	0.05383	0.01761	3.06	0.011	

Table 13. Stepwise regression results of migration rates (dependent variable) of hatchery coho salmon (N = 96) radio tagged at Bogus Creek and Shasta River through four index study reaches during spring, 2005. All analysis performed after loge-transformation of dependent variable; α to enter = 0.15.

Reach	Independent variable	Regression coefficients	*t*-value ($\beta = 0$)	Probability ($\beta = 0$)	R^2
1	Constant	-30.24			
	Day length	1.65	8.45	0.000	0.39
	FL	0.029	3.50	0.001	
2	Constant	-11.238			
	Flow	0.00044	4.00	0.000	0.40
	Release date	0.083	3.47	0.002	
3	Constant				na
4	Constant	-3.185			0.46
	Release date	0.054	3.06	0.011	

na: no predictor variable met criteria to enter the model

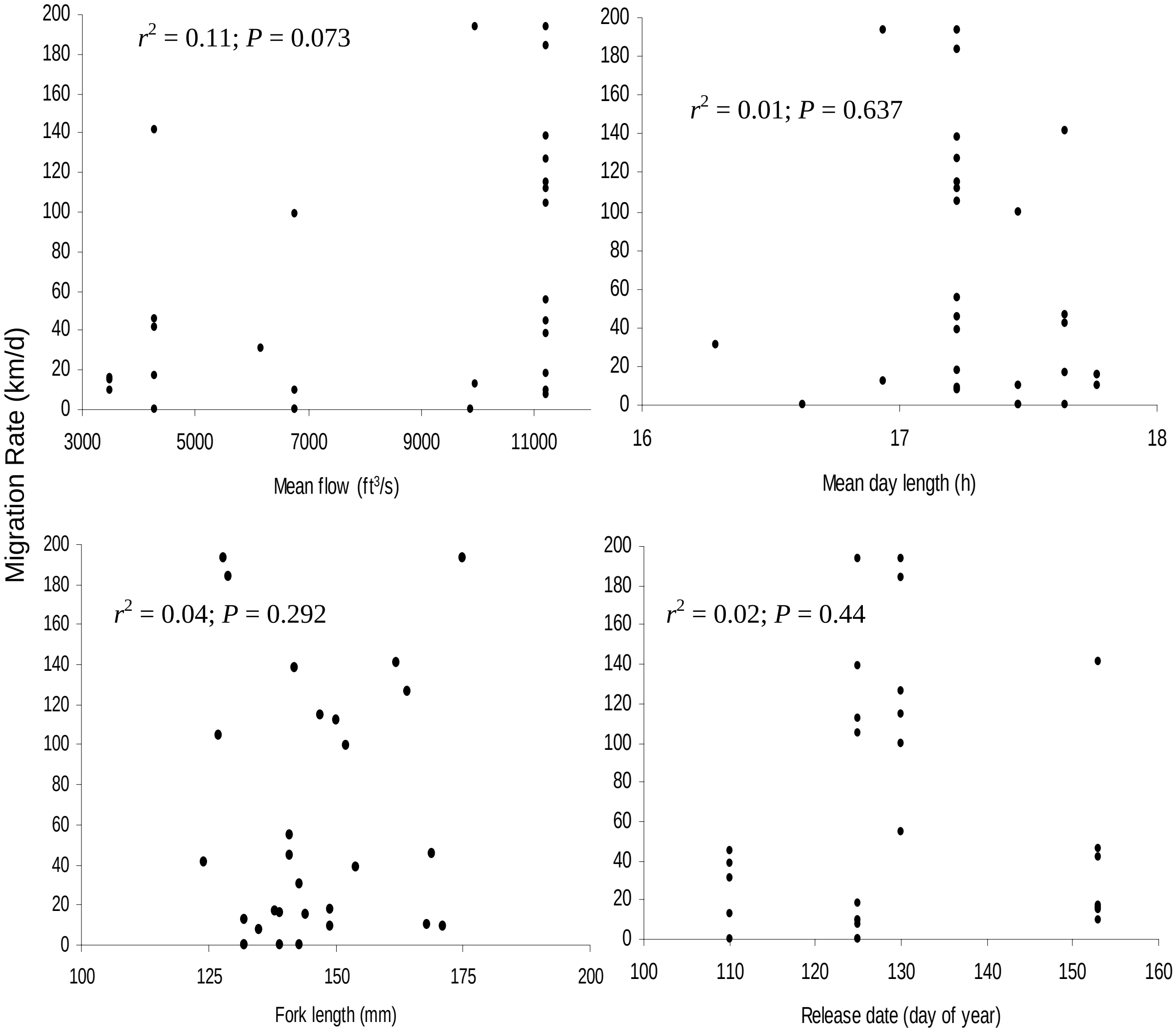

Figure 11. Relationships between migration rates of hatchery juvenile coho salmon within index reach 2 and independent variables during 2005. Solid circles represent non-transformed observed migration rates; r^2 and P-values are from bivariate analysis of $\log_e$-transformed values of migration rate.

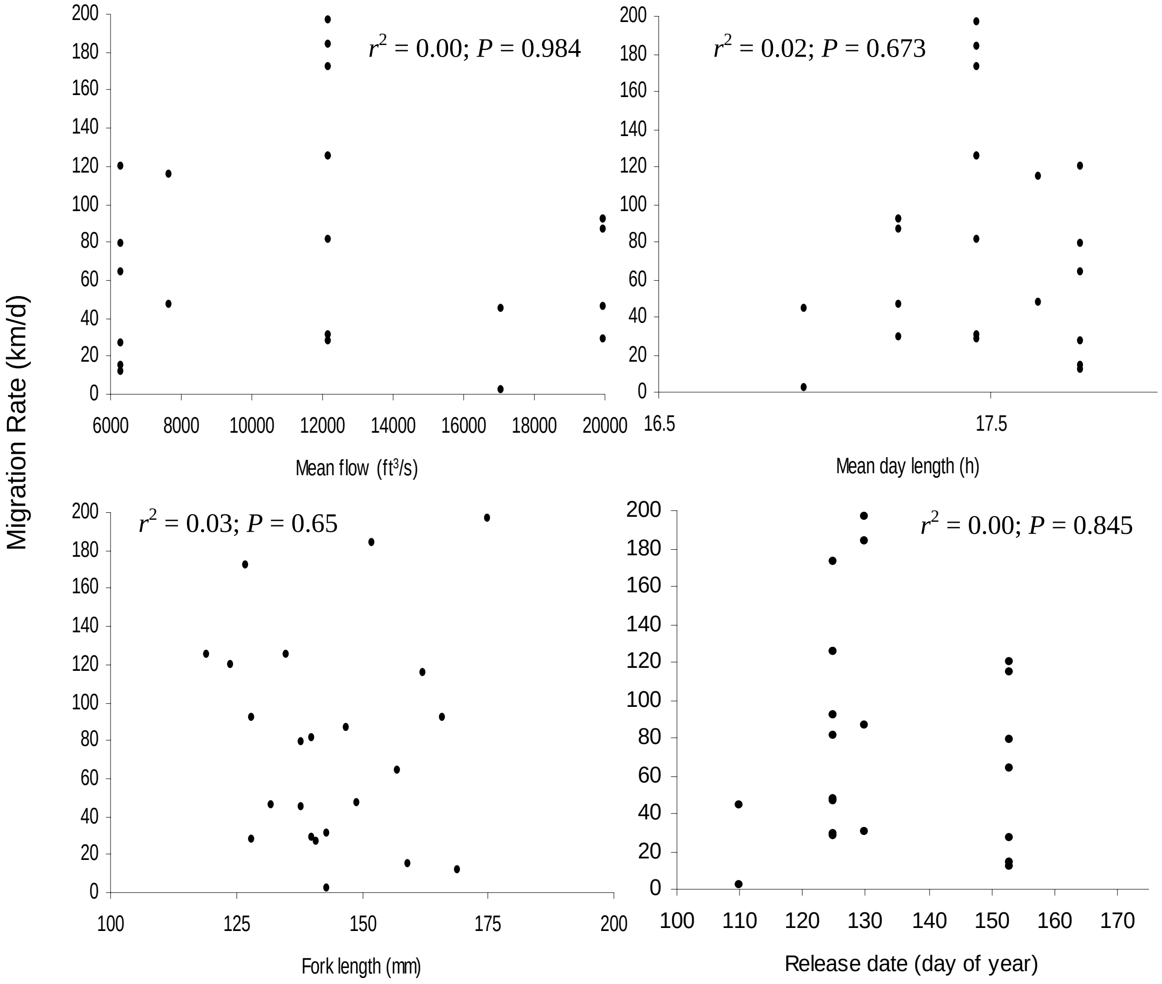

Figure 12. Relationships between migration rates of hatchery juvenile coho salmon within index reach 3 and independent variables during 2005. Solid circles represent non-transformed observed migration rates; r^2 and P-values are from bivariate analysis of $\log_e$-transformed values of migration rate.

Hatchery coho salmon index reach 4 (Trinity River to Estuary)

We detected 13 (14%) of the 96 radio-tagged coho salmon in the lower river (reach 4). A total of 13 migration rate estimates were calculated. The median migration rate of fish through this reach was 39.9 km/d (range = 3.6 – 145.6 km/d). The mean 7-d flows and day lengths experience by these fish ranged from 12,464 to 35,029 ft^3/s, and 16.9 to 17.7 h (Table 9).

Release date was the only predictor variable significantly correlated (positive relationship) with migration rate in the bivariate analysis and explained 45% of the variation in migration rate (Figure 13; Table 13) We could not develop a multivariate model that included flow or day length because these two variable were highly correlated with release date and had lower R^2 values.

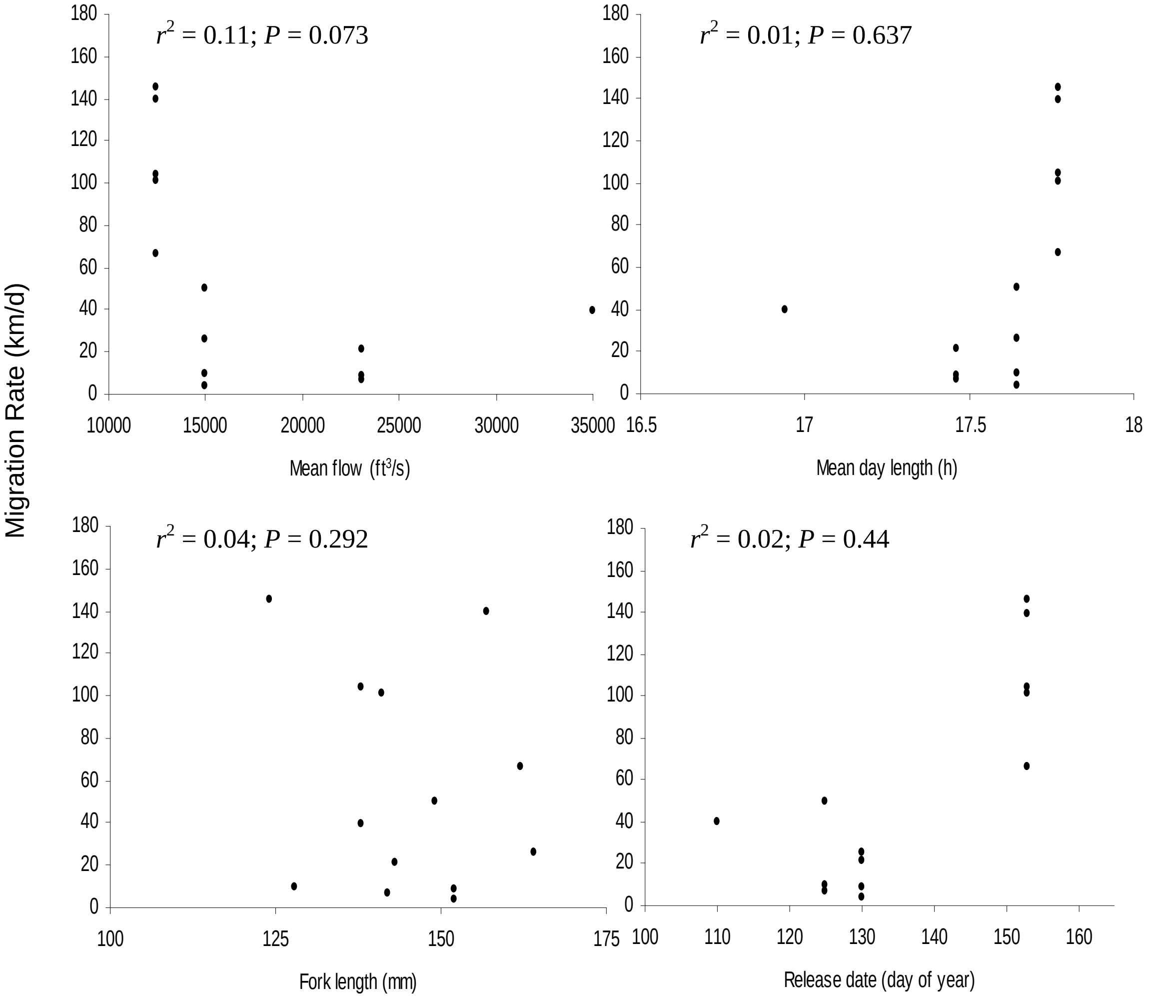

Figure 13. Relationships between migration rates of hatchery juvenile coho salmon within index reach 4 and independent variables during 2005. Solid circles represent non-transformed observed migration rates; r^2 and P-values are from bivariate analysis of $\log_e$-transformed values of migration rate.

Rearing behavior of hatchery coho salmon smolts

Four (4%) of the 96 hatchery fish tagged traveled a median distance of 12.3 rkm (range 0.25 – 178.65 rkm) and resided at a specific location for at least 24 h before resuming their downstream migration (Category 1). The median time these fish resided at rearing locations was 7.5 d (range 5 – 14 d), or an average proportion of 0.27 (range 0.15 – 0.39) of their total time at liberty. Two of the four category 1 fish were detected near the estuary.

Fourteen (15%) of the 96 hatchery coho salmon smolts tagged migrated downstream a median distance of 18.2 rkm (range 0 – 205.80 rkm) then remained at a specific location for the remainder of the tag-life (Category 2). The median number of days these tags were detected at their last location was 13.5 d (range 4 – 30 d). The proportion of the total time these tags were found at their last detection location averaged 0.50 (range 0.22 – 0.93).

Habitat use

We recorded a total of 112 habitat use observations during float surveys conducted on the mainstem Klamath River between Iron Gate Dam and the Scott River from 10 March to 29 May 2005. Tagged coho salmon smolts were most often observed in main channel sections of the river (106 out of 112 observations; Figure 14). Both hatchery and wild coho salmon smolts were detected primarily in pools (65%), but were also observed in low slope (20%), moderate slope (9%), and steep slope (4%) MHT's (Figure 14). Tagged coho salmon smolts were most commonly observed over sand or silt substrates (<0.1 in) that were prevalent in low velocity MHT's (Figure 15). Large cobble (9-12 in) had the second highest number of substrate use observations for wild fish (10 out of 45). Bedrock, large cobble, and medium cobble substrate types (6-9 in) comprised 45% (9 out of 20) of the substrate use observations for hatchery fish (Figure 15).

The majority (75%) of coho salmon located during this study were found near the edge of the stream channel, < 20 ft (6 m) from shore), and only 8 of 102 observations placed fish more than 32 ft (9.8 m) from shore (Figure 16). Instream positions of 59% of wild, and 47% of hatchery coho salmon we located were not directly associated with a functional cover source (Figure 14). Most of the fish not directly associated with cover were observed using shear zone micro-habitats (Figure 14), regardless of whether they were located on the stream edge or mid-channel. Shear zones were defined as a significant visible break in water velocity. Seventy percent of hatchery fish were observed within 14 ft (4.3 m) of a shear zones, and 70% of wild fish resided within 12 ft (3.7 m) of a shear zone (Figure 17). For fish using functional cover, object plus in water overhead cover (defined as < 18 in (46 cm) from the water surface), was most frequently (24% of all observations) recorded. The other four cover codes accounted for only 19% of all observations. When not using shear zones, coho salmon smolts were most often associated with dense aggregates of vegetation near shore, primarily willows (*Salix sp*.)

Approximately 75% (22 of 29) of the observations made for wild fish were in velocities ≤ 0.6 ft/sec. Hatchery coho salmon were observed in water velocities ranging from 0.2 ft/sec to 2.0 ft/sec (Figure 18). Water velocity measurements were limited to depths less than 8 ft due to limitations of the equipment used to measure velocity.

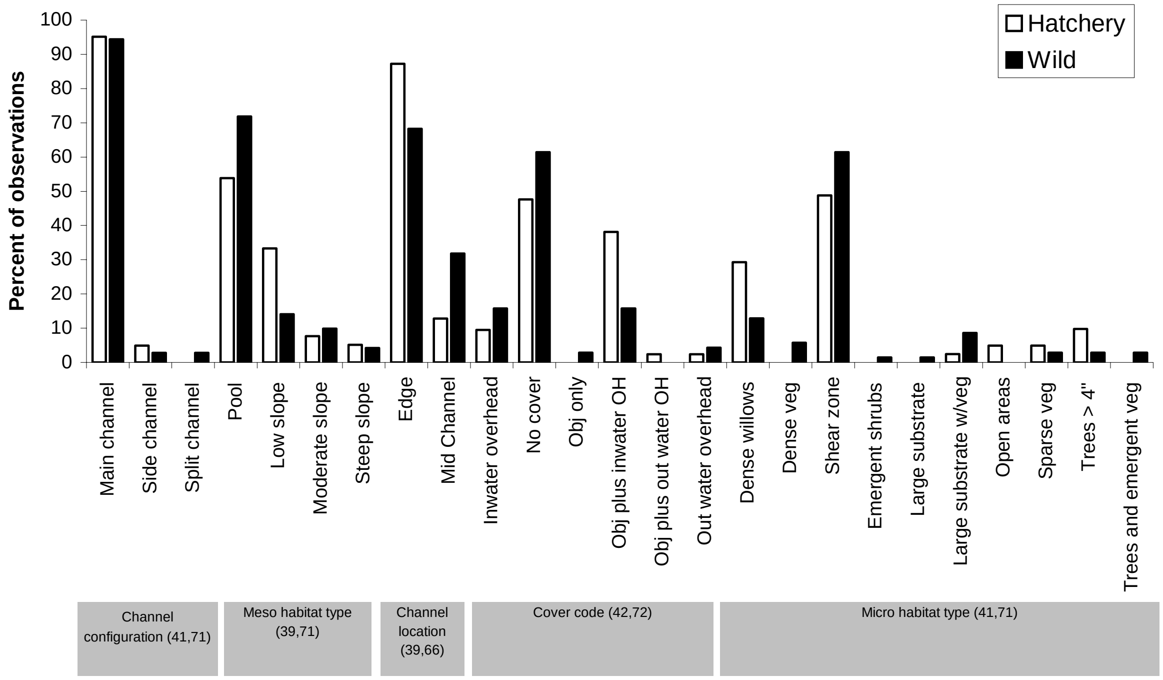

Figure 14. Channel configuration, meso-habitat type, channel location, and micro-habitat type associated with observations of hatchery and wild radio-tagged coho salmon in the mainstem Klamath River between Iron Gate Dam and the Scott River, 2005. Numbers in parentheses indicate the number of observations for hatchery and wild coho salmon for each category, respectively.

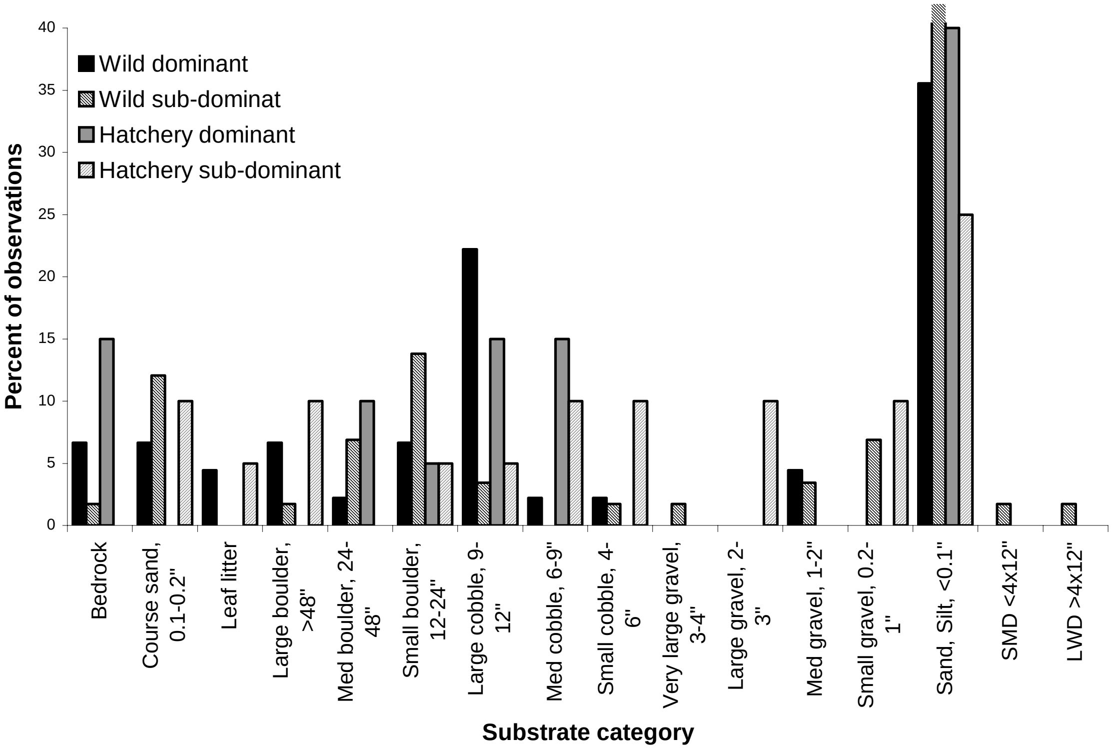

Figure 15. Frequency distribution of dominant and sub-dominant substrate types observed at locations of radio-tagged hatchery and wild coho salmon in the mainstem Klamath River between Iron Gate Dam and the Scott River, 2005.

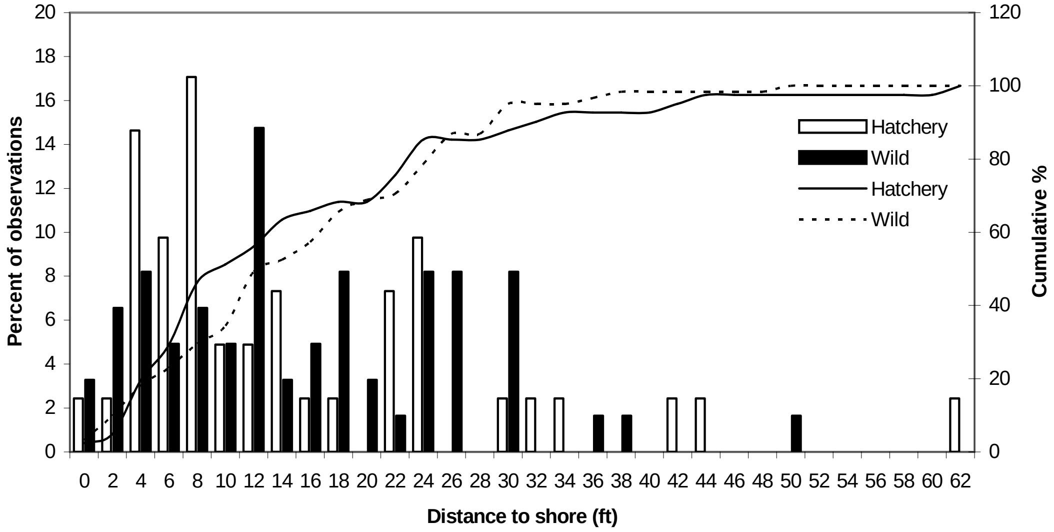

Figure 16. Frequency and cumulative frequency distributions of the distance to shore observed among radio-tagged coho salmon in the mainstem Klamath River between Iron Gate Dam and the Scott River, 2005. Number of observations for hatchery and wild fish were 41 and 61, respectively.

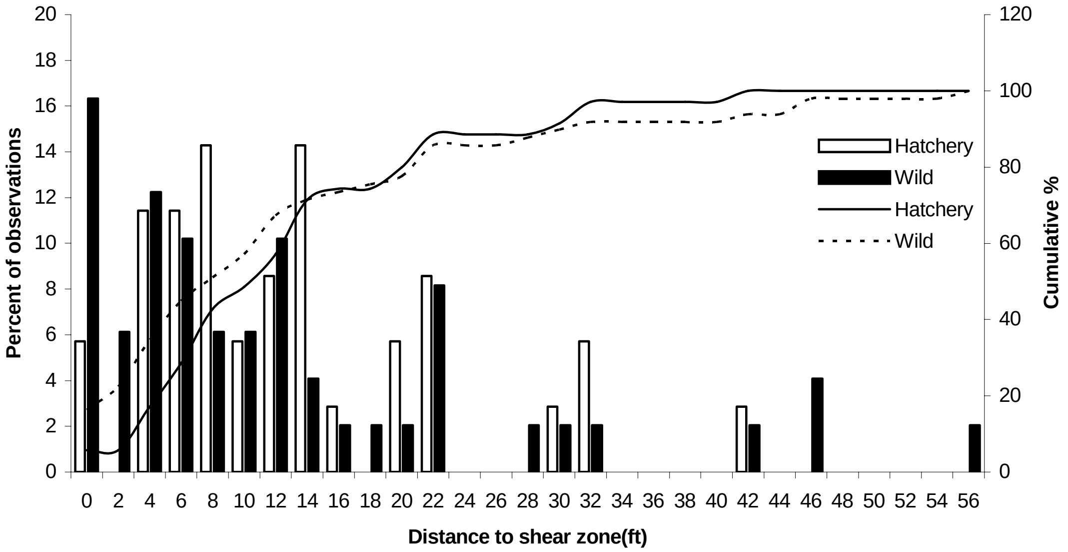

Figure 17. Frequency and cumulative frequency distributions of the distance to current shear zones observed among radio-tagged coho salmon in the mainstem Klamath River between Iron Gate Dam and the Scott River, 2005. Number of observations for hatchery and wild fish were 34 and 49, respectively.

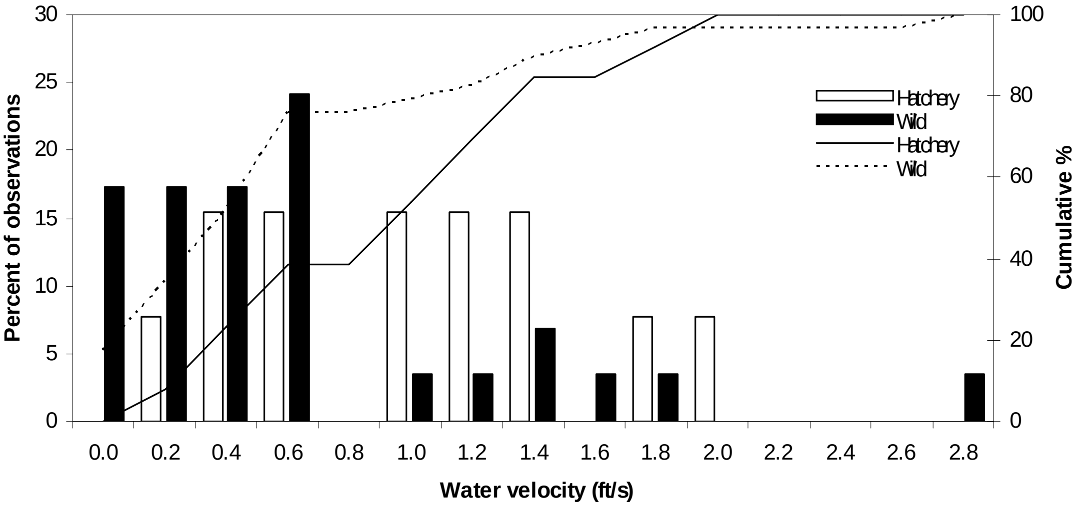

Figure 18. Frequency and cumulative frequency distributions of the water velocities observed at locations of radio-tagged coho salmon in the mainstem Klamath River between Iron Gate Dam and the Scott River, 2005. Number of observations for hatchery and wild fish were 13 and 29, respectively.

DISCUSSION

Efficacy of radio telemetry and design requirements of future studies

High capture probabilities observed at automated radio telemetry arrays in 2005 indicate that radio telemetry should be a valid method for estimating survival of juvenile coho salmon in the Klamath River downstream from IGD. This technique has been used successfully to estimate survival of juvenile salmonids in the Columbia and Snake rivers for the last several years (Counihan et al. 2002, Skalski et al. 2002). One distinct advantage of radio telemetry over mark-recapture methods based on passive tags (PIT tags, coded-wire tags, T-bar anchor tags, fin clips, etc.) is the high capture probabilities possible with this method, which in turn reduces the number of tagged animals required.

An implicit assumption of biotelemetry studies is that fish behavior and other vital biological processes are not significantly altered by the method of transmitter attachment or the presence of the transmitter. The effects of surgically implanted transmitters has been documented in several salmonid species (McCleave and Stred 1975, Moore et al. 1990, Moser et al. 1990, Adams et al. 1998b, Jepsen et al. 2001, Robertson et al. 2003). These studies provide useful insight on how transmitter size, type, and surgical technique affect feeding, swimming performance, physiology, transmitter retention, growth, and survival. Prior to conducting this study, a thorough review of published literature revealed a lack of information regarding the effects of surgically implanting radio transmitters into the coelomic cavity of juvenile coho salmon. To address this issue and to reduce uncertainty of results from our study, we concurrently examined the effects of surgically implanted radio transmitters on the survival, growth, and tissue response of 92 juvenile hatchery coho salmon (123-182 mm FL) at the IGH (Stutzer et al., 2005) Using transmitters that represented between 0.82 – 2.5 % of test fish body weight, no mortality occurred and growth of fish with surgically-implanted radio transmitters did not differ significantly compared to control fish over the 38-d study period. In summary, we found that by using proper surgical procedure, intraperitoneal implantation provides a suitable method for attaching radio transmitters for biotelemetry studies of juvenile coho salmon greater than 123 mm FL.

Our observations from 2005 coupled with the work of others cited herein provide strong support for the use of radio telemetry to estimate juvenile coho salmon survival in the Klamath River. The question remains, however, as to which survival model and design will produce the most precise and biologically meaningful results. Future studies should be implemented to allow comparisons to be made among several survival estimation models and designs. These include release-recapture (i.e., Cormak-Jolly-Seber) and known-fate models and both single-release and paired-release designs (Burnham et al. 1987).

Using the single-release design could result in survival estimates with good precision for a given sample size. For this design a single release point would be used, such as one slightly downstream from IGD. However, the effects of tagging and handling on fish after release cannot be separated from other factors affecting survival and could therefore bias the resultant survival estimate. This bias may occur if the effects of tagging and handling are expressed differently between the study reaches. To account for this potential source of bias, a paired-release design could be used to “cancel out” effects of tagging and handling between test and control groups. In a paired-release design, fish in the treatment group would be released the same as in the single-release design, but a control group would also be released at the downstream end of the river reach of interest, such as near the Shasta or Scott Rivers. This design is less efficient in terms of precision for a given sample size than the single-release model and is often challenging to implement. If capture probabilities are consistently near 1.0, a known-fate model can be used with these designs. Known-fate models are more efficient than release-recapture models in terms of precision for a given sample size because they estimate survival probabilities but not capture probabilities and thus have fewer sources of error than release-recapture models (release-recapture models estimate both survival and capture probabilities) (Burnham et al. 1987). Implementing a paired-release design in future studies would allow an assessment to be made about the validity of that design, the single-release design, and both release-recapture and known-fate models to determine which is most appropriate, depending on observed results and specific study goals.

Migratory behavior

Telemetry data collected in 2005 revealed variable patterns in migration behavior of radio-tagged juvenile coho salmon. For both hatchery and wild groups, median migration rates increased as fish traveled downstream through the first three index flow reaches and remained high through reach 4 (Figure 19). However, analyses of migration rates of radio-tagged fish within index flow reaches did not reveal a clear pattern of correlation with any single or combination of predictor variables in terms of the amount of variation explained or the nature of correlation. For example, our bivariate analyses revealed that the predictor variable flow explained the most variation in migration rate of wild coho salmon through index reaches 1 and 2 (Table 14). However, migration rate was positively correlated with flow in reach 1 and negatively correlated with flow in reach 2. In reach 3, release date was the only predictor correlated with migration rate (positive relationship), while in reach 4, the predictor variable fish length explained the most variation in migration rate (Table 14). Similarly, bivariate analyses of migration rates of hatchery fish did not reveal a clear pattern of correlation with predictor variables.

Berggren and Filardo (1993) documented that in multiple-regression analysis, surrogate variables of smoltification helped predict how quickly smolts migrated through index reaches. Contrary to these findings, our multivariate model analyses minimally increased the amount of variation in migration rate explained by the bivariate models, and in only one instance, revealed a significant correlation not apparent in the bivariate model (Table 14). This was likely the result of having to exclude predictor variables of smoltification from models due to multicollinearity with flow and because predictor variables did not significantly improve the fit of models. The multiple-regression analysis of Berggren and Filardo likely avoided the first of these problems by using indices of flow (reciprocal of flow averaged over the travel time in days, and absolute change in daily average flow over travel time) that were not as likely to be correlated to seasonal changes in predictor variables of smoltification.

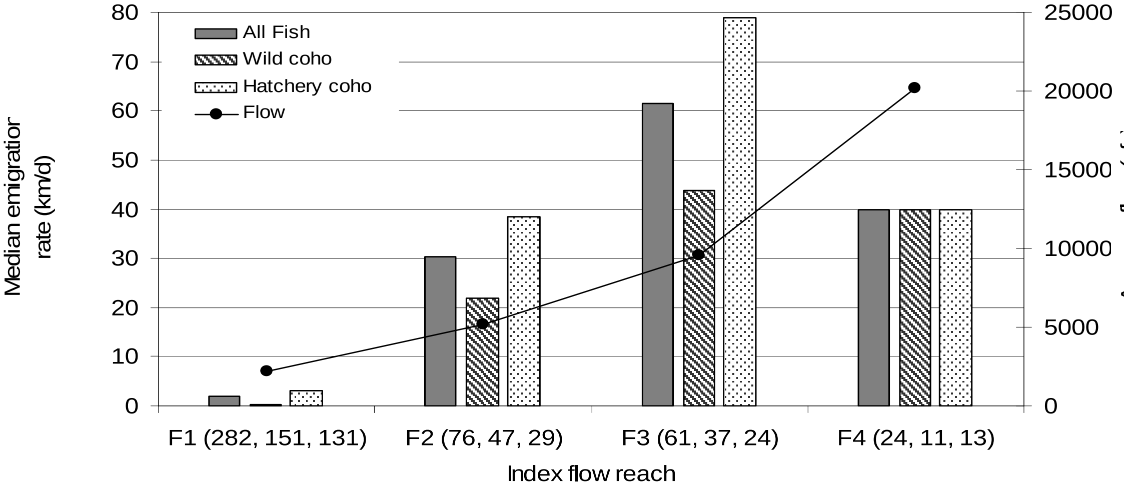

Figure 19. Median migration rates of wild and hatchery coho salmon smolts and both groups combined within four index flow reaches during spring 2005. Numbers in parentheses represent number of migration rate estimates for all fish, wild, and hatchery, respectively.

Table 14. Summary of most important predictor variables in migration rate analyses of radio-tagged juvenile coho salmon in the Klamath River, 2005. Numbers in parentheses represent corresponding r^2 or R^2; ns = no significant relationship for any predictor variable, probability (β = 0) >0.05.

Fish type	Index reach	Bivariate predictor	Multivariate predictors
Wild	1	Flow (0.25)	Flow, fish length (0.26)
	2	Flow (0.14)	Flow[a] (0.14)
	3	Release date (0.27)	Release date[a] (0.27)
	4	Fish length (0.66)	Fish length, day length (0.84)
Hatchery	1	Day length (0.34)	Day length, fish length (0.39)
	2	ns	Flow, release date (0.40)
	3	ns	Ns
	4	Release date (0.46)	Release date[a] (0.46)

[a] = no additional predictors allowed to enter model (α to enter = 0.15);

Hatchery fish, which were tagged latter in the study than wild fish, migrated through reach 1 more rapidly than wild fish tagged before May, even though flows were decreasing (Figure 20). Our results showed that for hatchery fish, flow was not correlated with migration rate for any reach. However, release date, day length, and water temperature were all significantly and positively correlated with migration rate in reach 1, and explained similar amounts of variation in migration rate (Figure 20). In contrast, flow was significantly and positively correlated with migration rates of wild fish in reach 1, and explained more of the observed variation in migration rate than any other predictor variable. This seasonal response may be a result of elevated levels of smoltification later in the season. Smoltification is a series of physiological changes preparing juvenile salmonids for the ocean environment (Hoar 1976). Past research has discovered that increased temperature and advanced photoperiod positively influence migration rate and timing in juvenile salmonids (Wagner 1974, Hoar 1976, Muir et al. 1994). Zaugg (1982) found that coho salmon held in a hatchery for delayed releases (June and July) migrated seaward more rapidly than fish released in May. Even though these late-release fish experienced a loss of both elevated gill Na^+-K^+ ATPase activity and silvery coloration prior to release, they were capable of rapid seaward migration and regeneration of elevated enzyme activity after release.

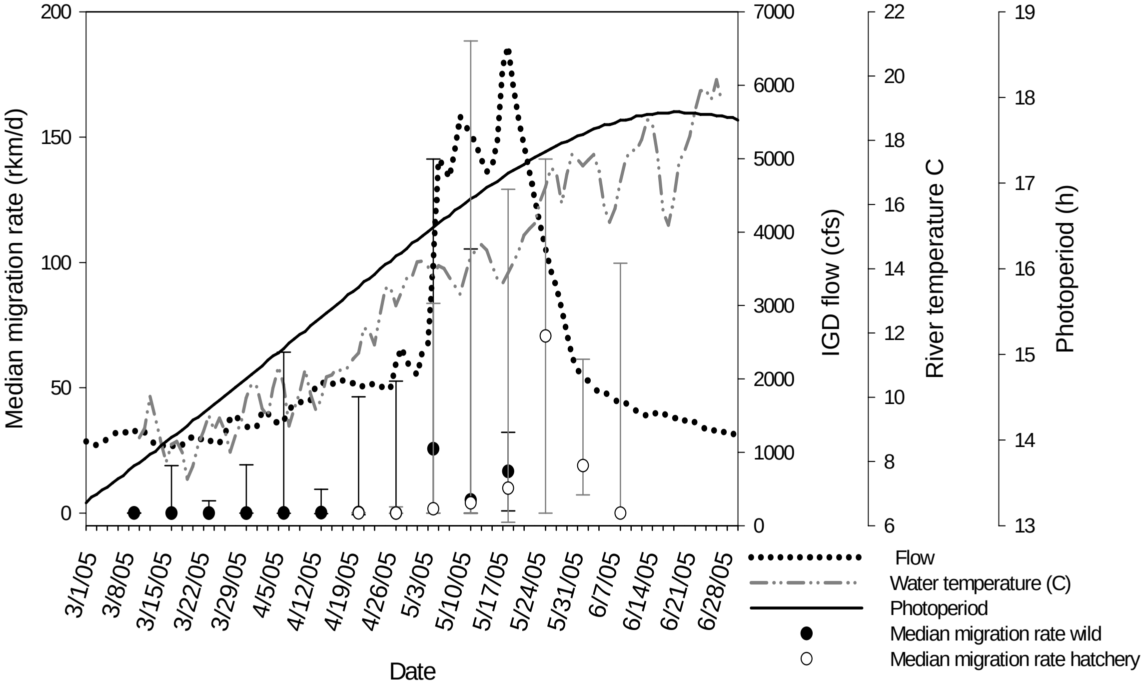

Figure 20. Mean migration rates of radio-tagged wild and hatchery coho salmon smolts through index reach 1 in relation to IGD discharge, river temperature, and day length during the 2005 study period. Points represent the mean migration rates of wild or hatchery fish within the reach at 7-d intervals; error bars show SEM.

We were unable to compare migration rates between wild and hatchery fish for the entire study period because most wild and hatchery fish were tagged at opposite time periods of the study. However, analysis of the wild and hatchery groups released at the Shasta River midway though the study revealed wild fish migrated through reach 1 significantly faster than hatchery fish released 48 h later (Table 8). Similarly, pooling migration data for both fish types across all reaches supported the conclusion that wild fish migrated downstream at a faster rate than hatchery fish. Outwardly, these data suggest it may be inappropriate to use hatchery fish as surrogates to make inferences about the migration behavior of wild coho populations in response to flow and other environmental conditions. However, this conclusion is tenuous because it is based upon the analysis of a single release event in which the data lacked normality and were unbalanced with regard to sample size. Some of the difference in migration rate between hatchery and wild fish in the 18-20 April paired-release test may be attributed to behavioral differences. Hatchery fish used in this study were released into the mainstem Klamath River shortly after being removed from hatchery raceways. The developmental condition of these fish may have differed from that of wild fish captured as they actively migrated out of tributaries (or hatchery fish captured during active seaward migration).

Giorgi et al. (1997) observed different migration rates of actively migrating yearling hatchery Chinook salmon *O. tshawytscha* in the Columbia River than did Berggren and Filardo (1993), who released fish directly from a hatchery. Results reported in Zaugg et al. (1985) demonstrated that coho salmon in the Columbia River system do not develop maximal hypo-osmoregulatory capability while confined in the hatchery environment, but appear to elicit a rapid increase in enzyme activity after release. Because the size and velocity of the Klamath River below IGD precludes the option of capturing sufficient numbers of actively migrating hatchery coho salmon smolt for radio tagging, ancillary information is needed to develop studies that evaluate the appropriateness of using hatchery fish as surrogates for wild fish. First, subsequent studies should measure temporal variation in gill ATPase levels of wild coho salmon emigrating from tributaries in the upper river as fish are being collected for radio tagging. Second, the relationship between gill ATPase activity and in-river exposure time of IGH coho salmon smolts should be well described. This information may allow researchers to modify procedures for releasing radio-tagged fish to promote similarity in the developmental state and migration behavior of wild and hatchery fish used in radio telemetry studies.

Although our results provide evidence that juvenile salmon behavior is not constant during downstream migration, further research in needed to elucidate how environmental conditions, developmental state, and habitat availability influence observed patterns in migratory behavior. For instance, the combination of available rearing habitat and developmental state of fish entering the mainstem river from tributaries may influence migration rate.

Although the slower migration rates we observed through reach 1 compared to other downstream reaches may be partially expected because of differences in river discharge, other factors may have contributed to the slower migration rates we observed. In a study investigating changes in physiological indices of smolting during seaward migration of wild coho salmon, Ewing and Roberts (1998) found that gill ATPase specific activity was significantly greater in migrants than in non-migrants. Assessing smoltification by directly measuring gill ATPase activity of tagged fish in the future may help explain the variation in migration rate we observed both within and between wild and hatchery coho salmon smolts. Additionally, researchers have identified other factors we did not include in our analysis that might help to explain the variation in migration rates we observed. These include differential behavioral responses to flow within the migration season, flow independent effects where fish migrate faster the longer they have been in the river (Zabel et al. 1998), and the magnitude of change in flow relative to base flows (Berggren and Filardo 1993).

We observed little compelling evidence that wild or hatchery coho salmon smolts showed a substantive response to discharge levels observed during this study. Even though flow was the most influential variable for wild coho salmon migration analyses in index reaches one and two, coefficients of determination were not particularly large (r^2 and $R^2 < 0.26$). Merely detecting a significant effect in a regression analysis does not guarantee the model has reliable predictive capability. Many of the regression models presented in Tables 10-13 are statistically significant, but the values of the coefficients of determination are uniformly low in all but one instance (r^2 and $R^2 < 0.65$), and likely have low predictive power (Prairie 1996). Further, the stability of regression models for the last index flow reach may be low because they relied upon small sample sizes. Least-squared linear regression analysis is inherently sensitive to outliers, and tests of significance and regression coefficients can be largely influenced by individual variates, especially in models using a small number of observations. The one case where we observed higher predictive power ($R^2 = 0.84$) was in the multivariate model including fish length and day length for wild fish in reach 4. This model suggests that the size of fish and photoperiod reliably explained the increase in observed migration rates of wild fish through reach 4 during the study. However, care must be used when interpreting this test statistic because it is generated from an analysis using only 11 estimates of migration rate.

The linear flow model we used for migration rate analysis assumes that increases in migration rate are directly proportional to increases in river velocity. This creates problems when trying to analyze data across reaches for two reasons. First it assumes that the velocity increase per unit of flow increase is constant across reaches. However, this is not the case because channel shape, gradient, and streambed roughness may vary between reaches. Second, the linear flow model implies that fish response to increased river velocities will not vary throughout the season. We attempted to resolve the first problem by developing regression models that analyzed the behavioral response of fish to changes in flow within multiple reaches where flow, gradient, and streambed roughness did not vary significantly. By incorporating other predictor indices (day length, water temperature, release date, and fish size), we had hoped to be able to detect seasonal migration effects. Procedures such as those described by Zabel et al. (1997) which compare travel time with a sequence of nested models using data at several observation sites from many release groups per year may enable the detection of complex migratory behavior that is not detectable with standard regression analyses.

Mainstem rearing

The migration behavior of fish observed in this study suggests that segments of the wild and hatchery coho salmon smolt populations we tagged may use the mainstem Klamath River for rearing in spring and early summer, prior to continuing their migration to the estuary. While the overall percentage of tagged individuals exhibiting category 1 rearing behavior was relatively low (11% of tagged wild and 4% of tagged hatchery fish), it is likely rearing in the mainstem Klamath River was greater than we report. Our criteria to determine rearing required a live fish to remain at a single location for at least 24 h, thereby omitting fish that may have reared while slowly moving downstream. Tagged fish that moved short distances downstream (less than about 100 m) between detections were therefore excluded as individuals exhibiting rearing behavior. It is also possible that a significant proportion of fish identified as exhibiting category 2 rearing behavior (16% of tagged wild and 15% of tagged hatchery fish) were indeed live coho salmon smolts rather than being tagged smolts in the stomachs of a mobile predatory fish. While difficult to assess due to depth and turbidity, this was visually confirmed by divers for two category 2 individuals that were observed holding and feeding in specific locations over the course of repeated detections until their tags expired.

An understanding of the habitat associations of juvenile coho salmon throughout the year is necessary to identify factors limiting smolt production and to assess the capacity of a stream or basin to produce smolts. Yearling coho salmon are largely thought to use the mainstem Klamath River as a migration corridor to the ocean during the months of March through June (Weitkamp et al. 1995). However, elevated tributary temperatures during the summer months (July – August) and the first winter freshets may also cause juvenile coho salmon to out-migrate into the mainstem river to seek refugia from thermal or high flow conditions. Therefore, coho salmon may use the Klamath River in some capacity for most months of the year and those that do may undergo physiological changes associated with smoltification that influence ocean survival while inhabiting the mainstem river.

Habitat use

Observations made during float surveys conducted in 2005 provide information on daytime habitat use of juvenile coho salmon during spring and early summer within the upper portion of the mainstem Klamath River (rkm 232 – 309.5). While our observations revealed that both hatchery and wild coho salmon smolts inhabited all mainstem MHT's, they were observed most often in types having low water velocities. In pool habitats, we found most radio-tagged coho salmon occupying shear zones. In contrast, radio-tagged coho salmon found in higher velocity habitats were most often associated with edge positions. Lotic waters with a high ratio of margin habitat to mid-stream area tend to be the most productive for juvenile coho salmon (Sandercock 1991). Seventy-five percent of the habitat use observations made in 2005 placed the location of fish within 20 ft (6.1 m) of the shoreline. We observed that radio-tagged coho smolts were not as closely associated with margin cover as Chinook and coho salmon fry, which often associate closely (<18 inches, 46 cm) to stream margin cover. Seasonal shifts in habitat use by juvenile coho salmon observed by others suggest fish tend to occupy deeper water habitats they grow (Nickelson et al. 1992). We found that fish inhabiting pools near shear zones were almost always in areas of relatively deep water. Frequently, the instream positions of these fish could not be directly associated with a specific cover source because of the depth and turbidity of the water. However, fluctuations in the strength of radio signals from fish swimming near shear zones suggests that these fish may have been using depth or substrate for cover intermittently between excursions towards the waters surface to feed. The research of others has documented the preference of juvenile coho salmon for low-velocity habitats to minimize energy expenditure (Mundie 1969), and to feed on drift suspended on the surface (Sandercock 1991, Hetrick et al. 1998). This information combined with our observations of habitat use suggests pools may be the most important habitats available to coho salmon smolts emigrating and rearing within the mainstem Klamath River during spring and early summers.

The seasonal availability of habitat for juvenile coho salmon rearing in the mainstem river can change vastly under varying flow conditions and adversely affect the ability of coho salmon to access preferred rearing habitats. Nickelson et al. (1992) observed definite seasonal shifts in habitat use by juvenile coho salmon in Oregon coastal streams. Similar to our findings, they found that during the summer, juvenile coho salmon were more abundant in pools of all types than they were in glides or riffles. However, during winter they observed highest juvenile coho salmon abundance in alcoves and beaver ponds; habitats that occur to a lesser degree within the mainstem Klamath River than in Oregon coastal streams. Changes in habitat use from summer to winter have been described primarily as a response to increased streamflows, decreased temperatures, and changes in fish size (Nickelson et al. 1992). If juvenile coho salmon in the Klamath River show distinct seasonal changes in habitat use, it will be difficult to predict smolt production potential of the basin or reliably determine the habitat limiting production based solely on an inventory of summer habitat. Nickelson et al. (1992) recommend that stream habitat be inventoried during the summer low-flow period and again during a winter base-flow period to generate more accurate estimates of production potential and habitats limiting production. Using an approach of comparing the habitat needs of coho salmon for spawning, spring rearing, summer rearing, and winter rearing, combined with estimates of survival between successive life stages may be useful towards identifying factors limiting coho salmon production within the Klamath Basin.

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APPENDIX

Appendix A. Habitat use criteria recorded for radio-tagged coho salmon during 2005 float surveys.

- Channel configuration
  - Main-channel
  - Side-channel
  - Split-channel
- Location in channel
  - Mid-channel
    - Edge
- Meso-habitat type
  - Pool
  - Low slope
    - Moderate slope
    - Steep slope
- Fish distance from shore
- Fish distance from shear
- Stream margin edge type (SMET)
    - Trees
    - Trees and emergent vegetation
    - Dense aggregates of willow/woody debris/berry
    - Emergent Shrubs
    - Open Areas
    - Sparce/Dense herbaceous vegetation
    - Large substrate/Rip-Rap/natural vegetation
    - Substrate/Bank influenced eddy
    - Backwater
- Substrate
    - Clay
    - Sand and /or Silt (<0.1’)
    - Coarse Sand (0.1-0.2”)
    - Small Gravel (0.2-1”)
    - Medium Gravel (1-2”)
    - Large Gravel (2-3”)
    - Very Large Gravel (3-4”)
    - Small Cobble (4-6”)
    - Medium Cobble (6-9”)
    - Large Cobble (9-12”)
    - Small Boulder (12-24”)
    - Medium Boulder (24-48”)
    - Large Boulder (>48”)

Appendix A, (continued). Habitat use criteria recorded for radio-tagged coho salmon during 2005 float surveys.

- Cover Code
  - No Cover
  - Object only
  - In water overhead
  - Out water overhead
  - Object and in water overhead
  - Object and out of water overhead
- Vegetation Codes
  - Filamentous Algae
  - Non Emergent Rooted Aquatic
  - Emergent Rooted Aquatic bull rushes
  - Grass
  - Sedges-cattails
  - Cockle burrs
  - Grape Vines
  - Willows
  - Berry Vines
  - Trees < 4” dbh
  - Trees > 4” dbh
  - Rootwad
  - Aggregates of small vegetation (<4”)
  - Aggregates of large vegetation (>4”)
  - Duff, leaf litter, organic debris
  - Small Woody Debris (< 4”x 12’)
  - Large Woody Debris (> 4”x 12’)
- Mid column water velocity
  - Water Depth at fish