PREDATION BY HATCHERY STEELHEAD ON NATURAL SALMON FRY IN THE UPPER-TRINITY RIVER, CALIFORNIA

by

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ABSTRACT

Predation by Hatchery Steelhead on Natural Salmonid Fry in the Upper-Trinity River, California

Seth W. Naman

Hatchery fish have been implicated in the decline of stocks of naturally produced anadromous salmonids in the Pacific Northwest. I investigated the extent of predation by hatchery steelhead on naturally produced salmonid fry in the upper-Trinity River, California. During spring of 2007, 315 residualized hatchery steelhead and 1,636 juvenile hatchery steelhead were captured and examined for the presence of salmonid fry in the gut. Residualized steelhead consumed 435 salmonid fry and 2,685 salmonid eggs. Juvenile hatchery steelhead consumed 882 salmonid fry. Predation by juvenile hatchery steelhead was significantly greater near a side channel where a high percentage of adult salmonids were known to spawn. I used mark-recapture techniques to estimate the population of residualized hatchery steelhead and PIT tag recoveries to estimate the population of juvenile hatchery steelhead. Using the population estimates and predation rates, I estimated that 24,194 [95% CI = 21,066-27,323] salmonid fry and 171,018 [95% CI = 155,272-186,764] salmonid eggs were consumed by 2,302 residualized hatchery steelhead in 21 days from 10 February to 2 March 2007. Excluding the results from the side channel, I estimate that 437,697 juvenile hatchery steelhead consumed 61,214 [95% CI = 43,813-78,615] salmonid fry in 30 days from 28 March to 26 April 2007. Assuming

a constant population of 1,500 juvenile hatchery steelhead in the side channel during the 30 day period, an additional 49,445 salmonid fry were consumed. Managers should carefully consider all of the risks to naturally produced fish populations from hatchery fish in order to determine if the effects of hatchery releases are consistent with management goals.

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INTRODUCTION

Although several researchers have concluded that predation can influence the population dynamics of anadromous salmonids (Mather 1998), little is known about the extent to which hatchery salmonids prey upon naturally produced salmonids. Nonetheless, millions of hatchery salmonids are released into rivers throughout the western United States annually (Levin et al. 2001). Several researchers have studied competition between hatchery and naturally produced salmonids (e.g. Pollard and Bjornn 1973, McMichael et al. 1997, Fleming et al. 2000, Kostow and Zhou 2006), but predation by hatchery salmonids on naturally produced salmonids remains virtually undocumented in the peer-reviewed literature. Several studies have examined predation by naturally produced salmonids on naturally produced salmonids (e.g. Ruggerone and Rogers 1992, Beauchamp 1995), and others have investigated smallmouth bass predation on salmonids (e.g. Fritts and Pearsons 2004, Naughton et al. 2004), but none specifically address predation by hatchery salmonids on naturally produced salmonids. However, there are a variety of contract reports and technical memoranda on the subject (Table 1). Most of these studies documented low rates of predation, and those that have attempted to estimate the total number of fry consumed have reported relatively low numbers (e.g. Cannamela 1993).

Each year, Trinity River Hatchery releases roughly 800,000 steelhead smolts and 500,000 coho salmon smolts at the base of the Lewiston Dam, directly into an important

Table 1. Review of hatchery steelhead predation studies.

Citation	River System	State	Methods	Sample size	Fry ingested (n)	Fry/Stomach
Beauchamp 1995	Cedar	Washington	Electrofishing	18	0	0.00
Canamella 1993	Upper Salmon	Idaho	Hook and line/electrofishing	6,762	10	0.00
Hawkins and Tipping 1999	Lewis	Washington	Seine	74	1	0.01
Hawkins and Tipping 1999	Lewis	Washington	Seine	110	2	0.02
Hawkins and Tipping 1999	Lewis	Washington	Seine	48	52	1.08
Jonasson et al. 1994	Imnaha/Grande Rhonde basins	Oregon	Hook and line/electrofishing	358	1	0.00
Jonasson et al. 1995	Imnaha/Grande Rhonde basins	Oregon	Electrofishing	175	2	0.01
Martin et al. 1993	Lower Snake (Tucannon)	Washington	Hook and line	1,713	3	0.00
Whitesel et al. 1993	Imnaha/Grande Rhonde basins	Oregon	Screw trap/electrofishing	611	8	0.01

spawning region. The release occurs at a time when many naturally spawned fry and juveniles are emerging from spawning gravels or rearing. Because of the size differential between predator and prey (Pearsons and Fritts 1999) and the spatial and temporal overlap of predator and prey (Mather 1998; Hatchery Scientific Review Group 2004) there is strong potential for predation by hatchery-reared steelhead to significantly impact the abundance of natural salmonid fry.

The upper Trinity River is relatively clear, often averaging less than 2 nephelometric turbidity units (NTU) and sometimes less than 1 NTU during the Chinook salmon and coho salmon fry emergence period. Studies have shown that low turbidity promotes high foraging efficiency by piscivorous fishes (Gregory and Levings 1998; Robertis et al. 2003). However, no estimates of the amount of naturally produced salmonid fry consumed by hatchery salmonids in the Trinity River are available.

There is currently no information available on the extent to which hatchery steelhead residualize in the Trinity River. Hatchery reared steelhead are known to residualize in river systems throughout the western United States (Beauchamp 1995; Viola and Schuck 1995, McMichael and Pearsons 2001). They residualize in greatest numbers near the site of release, decreasing in number as the distance from the point of release increases (Viola and Schuck 1995, McMichael and Pearsons 2001). Negative impacts from predation (Hatchery Scientific Review Group 2004), competition (McMichael et al. 1997), or genetic interactions (Reisenbichler and Rubin 1999), may affect naturally spawned salmonids resulting from the presence of residualized hatchery steelhead. Hatchery reared steelhead have also been shown to be more aggressive than

wild steelhead (Berejikian et al. 1996, McMichael et al. 1999, McMichael and Pearsons 2001), which may exacerbate the effects of competition between hatchery and wild fish. In the uppermost 3.2 km of Trinity River, residualized hatchery steelhead cannot be legally removed by fishermen, as fishing regulations specify that the area is “fly only” and “catch and release only.”

The objectives of this study are to 1) estimate the proportion of piscivores in the residualized hatchery steelhead population and juvenile hatchery steelhead population of the upper Trinity River; 2) estimate the rate (fry/piscivore) at which piscivores in the residualized hatchery steelhead population and juvenile hatchery steelhead population prey upon naturally produced salmonid fry; 3) estimate the population sizes of residualized hatchery steelhead and juvenile hatchery steelhead; and 4) estimate the number of naturally produced salmonid fry consumed by residualized hatchery steelhead and juvenile hatchery steelhead on the upper Trinity River, in the study reach, during the period of study. This information could be used to help guide hatchery policies and is critical to understanding one of the impacts that Trinity River Hatchery may have on natural populations of salmonids.

STUDY SITE

The study area extended from Lewiston Dam, downstream 3.2 km to Old Lewiston Bridge (Figure 1). Trinity River Hatchery is located at the base of the dam, which is the terminus of anadromous fish migration in the Trinity River. This study reach is characterized by a largely confined channel and an alternating series of runs, pools, glides and riffles. Mean channel width is 30.2 m with a mean channel slope of 0.3% (Trinity River Flow Evaluation 1999). Throughout much of fall and winter, discharge from Lewiston Dam is at a base flow of approximately 8.5 m^3s^{-1}, and water from Trinity and Lewiston reservoirs keeps daily maximum river temperature, even in the heat of the summer, at approximately 12°C (Trinity River Flow Evaluation 1999). Beginning in the end of April, discharge from Lewiston Dam increases in accordance with the Trinity River Flow Evaluation (Trinity River Flow Evaluation 1999) to serve a variety of fisheries and geomorphological functions. Discharge then decreases, generally in the end of July, to 12.7 m^3s^{-1}, and remains at this level through the summer and fall until the beginning of October when it returns to a base flow of 8.5 m^3s^{-1} (Trinity River Flow Evaluation 1999).

Elevation of the study reach is roughly 549 m. Summers are hot and dry followed by a mixture of rain and snow in the winters, typical of northern-California mid-elevation regions that are on the cusp of coastal and arid climates. Average annual precipitation for Weaverville, California, located approximately ten miles northeast of the study area, is 92.8 cm of rain and 45.2 cm of snowfall (National Weather Service 2008).

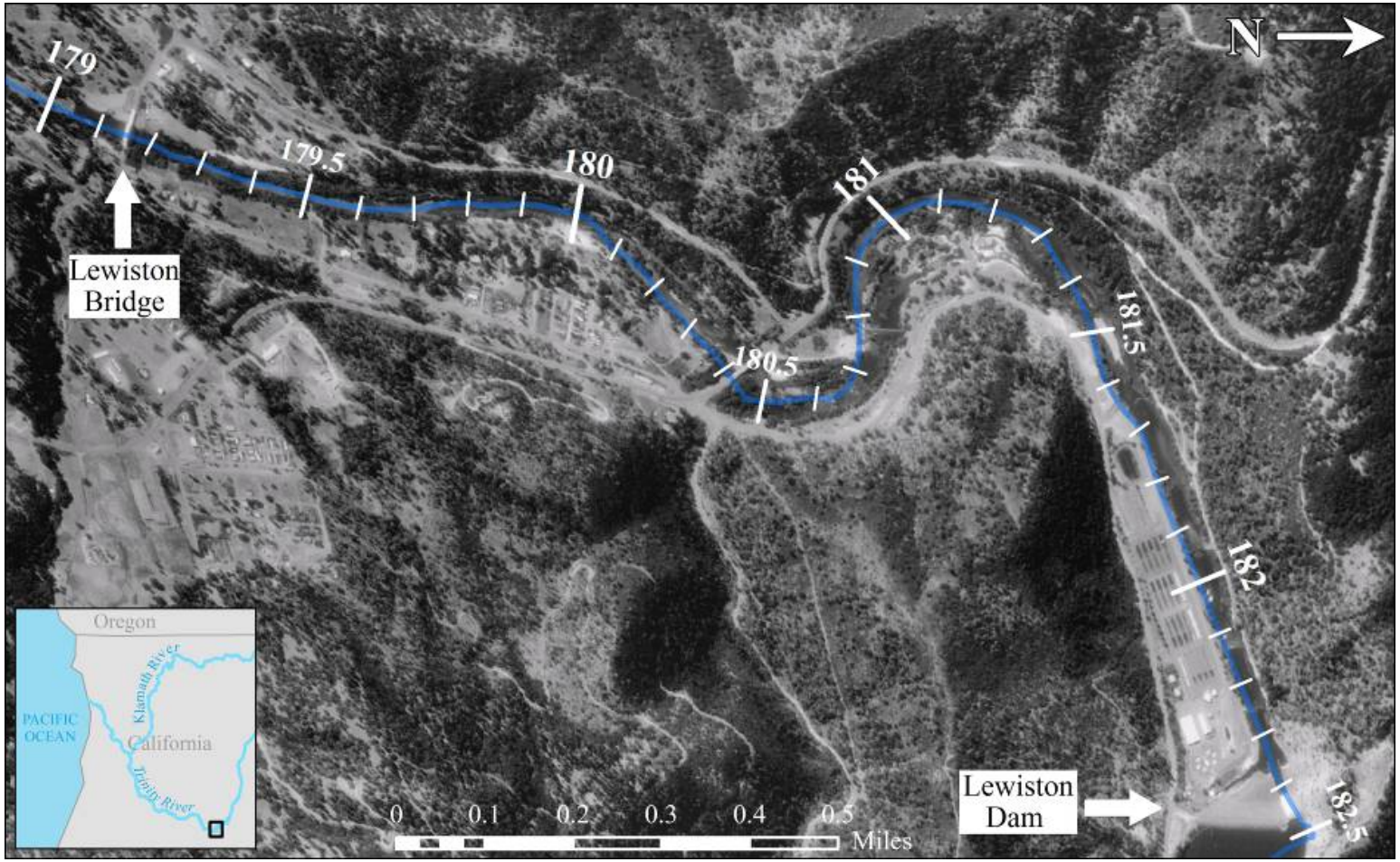

Figure 1. Map of the study location, and river kilometers (in white) on the upper-Trinity River, California. River kilometers increase in an upstream direction and begin at zero at the confluence of the Trinity and Klamath rivers near the town of Weitchpec, California.

The study reach is inhabited by spring- and fall-run Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), steelhead (*O. mykiss*), Pacific lamprey (*Lamptera tridentata*), and brown trout (*Salmo trutta*). Coho salmon are listed under both the federal Endangered Species Act (Good et al. 2005), and the California Endangered Species Act (California Department of Fish and Game 2002).

The upper river provides spawning grounds for anadromous species which are harvested by tribal, recreational and sport fishermen. In the uppermost 3.2 km of the Trinity River, the terminus of anadromous fish migration, estimated redd totals for 2006 were 2,302 redds for Chinook salmon and coho salmon combined. This represents 53% of all redds that were counted from the dam to the North Fork Trinity River, 63.4 km downstream. This high concentration of redds in this section of river is typical for any given year (United States Fish and Wildlife Service 2007). While no data are recorded on the number or distribution of steelhead redds, it appeared to me that a similarly high percentage of the total number of redds were concentrated in the uppermost 3.2 km of river (personal observation).

According to data collected by the California Department of Fish and Game (CDFG) at weirs operated on the Trinity River, the majority of anadromous spawners are of hatchery origin. Returns of hatchery coho salmon have been relatively robust in recent years, but the proportion of natural coho salmon returning to the Trinity River has remained around 10% for many years (Trinity River Flow Evaluation 1999; California Department of Fish and Game 2005). There have been relatively strong runs of hatchery steelhead in the recent past, but the proportion of natural fall-run steelhead returning to

the Trinity River has remained around 20% of the total for many years (Trinity River Flow Evaluation 1999; California Department of Fish and Game 2005). The majority of both spring- and fall-run chinook salmon adults are also of hatchery origin, with natural Chinook salmon making up roughly 25% of the total (Trinity River Flow Evaluation 1999; California Department of Fish and Game 2005).

METHODS

General Field Methods

Prior to release, all hatchery steelhead are marked by adipose fin excision at Trinity River Hatchery, making the distinction between naturally produced steelhead, few of which were captured, and hatchery steelhead, straightforward. Prior to 15 March, any fin-clipped steelhead present in the study reach, excluding anadromous steelhead, were characterized as a residualized hatchery steelhead. Residualized hatchery steelhead were sampled from 6 February to 28 February 2007 and juvenile hatchery steelhead from 27 March to 26 April 2007. Sampling by the Yurok Tribal Fisheries Program in 2005 indicated that the maximum size of residualized hatchery steelhead was roughly 500 mm (Yurok Tribal Fisheries Program 2008). In addition to this size threshold, behavioral and morphological traits were used to distinguish between residualized and anadromous hatchery steelhead. After 15 March, hatchery steelhead that were 250-500 mm in fork length, excluding anadromous steelhead, were considered to be residualized. I used a cut off of 250 mm because only 3 out of 316 residualized hatchery steelhead captured prior to the release of juveniles on 15 March were less than 250 mm. Scale samples were collected from 99 residualized hatchery steelhead to determine age classes and to verify that none of the steelhead identified as residuals showed signs of ocean entry or ocean growth in scale patterns (Holtby et al. 1990). No attempt was made to determine the age of residualized hatchery steelhead considered to be older than age 3.

Three sites were sampled on a weekly basis throughout the duration of the study: Old Lewiston Bridge (rkm 179), Old Weir Hole (rkm 180.7) and the hatchery area (rkm 182.0, Figure 1). River kilometers begin at zero at the confluence of the Trinity and Klamath rivers near the town of Weitchpec, California and increase in an upstream direction. These sites were roughly located at the downstream end, middle, and upstream end of the study zone. Additionally, one or more of the following sites were sampled on a weekly basis: River Oaks Resort (rkm 180.0), New Lewiston Bridge (rkm 180.4), riffles between Old Weir Hole and New Lewiston Bridge (180.6) and Bear Island Area (rkm 181.5). Within the study reach this regime gave equitable spatial distribution to sampling locations.

Steelhead were captured using hook and line with wet or dry flies. Fish were almost exclusively taken using flies (either dry or wet invertebrate patterns). Using lures might have biased the data because fish that strike lures may have a greater propensity toward piscivory than the population as a whole. It should be noted that great care was taken in selecting small flies (≤ size 16 hooks) so that small fish could be caught as effectively as larger ones. The use of hook and line made it possible to collect fish from a wide range of locations and habitat types that would be inaccessible using other methods such as seining or electrofishing.

On four occasions, the sampling crew captured juvenile hatchery steelhead with hook and line, and then captured juvenile hatchery steelhead with a seine net or backpack electrofishers, generally in the same locale on the same day. This was done in order to

compare the rate of predation between fish that were captured using hook and line and other methods, to check for bias resulting from capturing fish with hook and line.

When sampling fish with electrofishers, a single pass was utilized, with personnel moving upstream expeditiously because the electrical current can disable fry and make them easy targets for hatchery steelhead in the area. If temporarily disabled fry float downstream during the electrofishing process and are consumed by hatchery steelhead downstream, and those steelhead are captured and examined within the next 25-30 hours, one might overestimate the number of fry consumed.

In addition to the comparisons of sampling methods, I checked for differences in size between fish that were captured in the river and that of the hatchery population as a whole. Size difference could bias the estimate of total number of fry consumed. On 14 March 2007, one day prior to the release of juvenile hatchery steelhead from Trinity River Hatchery, 50 fish were weighed and measured from each of ten raceways for comparison with the size of individuals captured by hook and line during the first week of study. Testing was constrained to the first week of study because growth, high mortality of small fish, emigration of larger fish, high mortality of sick or weak fish, etc., might change the population characteristics over the course of the study from the original characteristics of the hatchery population.

Captured fish were placed in five gallon buckets before being transferred to a live well that was placed directly in the river. They were examined within 2 hours of being captured. Fish were measured to fork length, visually examined for body morphology, spotting, coloration and skin silvering, then given a smoltification rating of not smolting,

transitional, or smolting (Viola and Schuck 1995). Both body morphology (Beeman et al. 1995) and skin reflectance (Haner et al. 1995, Ando et al. 2005) have been successfully used to discriminate between fish that are smolting, and those that are not. I compared condition of juvenile hatchery steelhead among the smolting categories using Fulton's K (Cone 1989). Prior to analysis and testing, each group was tested for isometric growth by regressing the natural log of fork length on the natural log of weight to determine if the slope differed significantly from three (Cone 1989). Additionally, I tested if the regressions of K on fork length were significantly different than zero, in order to check for dependence of condition on fish length (Cone 1989).

A 7.6 L hand pump garden sprayer was used to perform pulsed gastric lavage (Light et al. 1983). Stomach contents were flushed onto a white dish, examined for the presence of fish or fish parts, and recorded as empty, or containing one or more of the following: inorganic or organic material, invertebrates, salmonids, and (or) other fish species. After examination, captured steelhead were revived and released except for approximately 20 samples that were sacrificed to check the effectiveness of the lavage technique. All salmonid fry detected in samples of stomach contents were enumerated.

I did not attempt to identify consumed salmonid fry to species. Both Chinook salmon fry and coho salmon fry were prevalent in the study reach during this study, with steelhead fry beginning to emerge from the spawning gravel towards the end of the study period.

Consumed fry were known to be of natural origin for several reasons. Chinook salmon are not released from the hatchery until June on the Trinity River, whereas this

study was conducted from February to May. Hatchery Chinook salmon are also released at a size that is typically larger (roughly 80 mm) than the size of consumed salmonids, which were generally less than 50 mm. Additionally, 100% of coho salmon and steelhead are marked before being released from Trinity River Hatchery, making it easy to distinguish between these hatchery "smolts" and naturally produced eggs, alevin, and fry.

Residualized hatchery steelhead population estimation

Upon examination, all residualized hatchery steelhead were marked with a fluorescent yellow 16 mm Petersen Disc™ applied below the dorsal fin, except for those considered to be smolting or injured. This allowed for re-sighting of marked fish, making a mark-recapture population estimate possible. I used a modified Petersen estimator (Seber 1982) to estimate the number of residualized hatchery steelhead that were present in the reach during the study period. The marking of fish began on 12 February. After the completion of gastric sampling on 1 March, fish were re-sighted using four divers swimming abreast of each other. I assumed no mortality or immigration or emigration of residualized hatchery steelhead during this 17 day period. Nominal mortality of residualized hatchery steelhead (naturally caused or otherwise) would have little bearing on results of this study. It is unlikely that there were large scale movements into or out of the study reach during the period of study by these non-migratory fish. For example, river discharge and temperature, which might influence movement of residuals, were generally constant during the period of study.

Juvenile steelhead population estimation

At Trinity River Hatchery, steelhead eggs are taken in winter and spring. Progeny are raised for approximately one year before being released the following spring. The release strategy is volitional, beginning on 15 March each year and continuing for 10-14 days, at which time hatchery personnel force the remaining fish from the hatchery. This makes the estimation of the number of juvenile steelhead in the study reach at any given time inherently difficult as the proportion that exits the hatchery volitionally, and the proportion that is forced out, are not known.

In order to estimate the population of juvenile hatchery steelhead in the study reach on a daily basis, 991 steelhead were implanted with 23 mm half duplex Passive Integrated Transponder (PIT) tags (Zydlewski et al. 2006). This tagging occurred on 5 February and 6 February 2007, approximately 6 weeks prior to the beginning of volitional release from the hatchery. Juvenile hatchery steelhead in 9 of 10 raceways received approximately 110 PIT tags. The other raceway contained fish that were too small (≤ 100 mm) at the time to implant with the 23 mm PIT tags. The number of hatchery steelhead in each raceway at the time of tagging is known as they are hand counted and marked with an adipose fin clip by hatchery personnel and staff from Hoopa Valley Tribal Fisheries.

To gain an understanding of the proportions and timing of juvenile hatchery steelhead that entered and exited the study reach, two antennas were placed in the hatchery flume (hatchery antennas) and 2 antennas spanning the river were placed near the end of the study reach (river antennas). Sampling of juvenile hatchery steelhead

began on 27 March 2007, the day that personnel at Trinity River Hatchery forced steelhead out of the hatchery that remained in raceways after the two week volitional release period.

The two antennas that made up the hatchery array were constructed of wood frames and measured approximately 0.9 m by 1.3 m. Each antenna was wrapped in three loops of eight gauge speaker wire which fit into channels that were routed into the wood frames. Antennas slid neatly into pre-existing slots contained within the walls of the flume, and spanned both the width and depth of the flume.

The first river antenna was installed on 19 March, the second on 21 March. This array consisted of two antennas that were 15 m apart, one measuring 13.6 m and the other 18.2 m wide. The distance between the upper and lower loops of the antennas was approximately 0.45 m. The top portion of the antenna loop remained below the water surface to avoid ensnaring boaters. The antennas were formed from a single loop of 8 gauge speaker wire enclosed in standard garden hose that was attached to steel cable affixed to trees on each stream bank. Rock walls were constructed on the edges of each antenna where they met the stream bank to keep hatchery steelhead from migrating around the side of the antennas. This made the path efficiency (Zydlewski et al. 2006), the probability that a fish swimming downstream will pass through the antenna, approximately 100%. Antenna efficiency at both the hatchery and river arrays was tested weekly, sometimes bi-weekly, with test tags placed in oranges, neutrally buoyant pieces of wood, and on the end of an eight foot pole.

Using data from the hatchery antennas, I determined the proportion of PIT-tagged fish that were forced out of the hatchery. I then multiplied this proportion by the number of hatchery steelhead that were in the 9 raceways which received tags such that

$$\hat{S}_1 = \hat{P}_f \times 729{,}760, \tag{1}$$

where $\hat{P}_f$ is the proportion of PIT-tagged fish that were forced out of the hatchery, $729{,}760$ is the total number of fish in each of the 9 raceways that contained marked fish and $\hat{S}_1$ is the number of steelhead that entered the study reach from the hatchery on the day that sampling of juvenile hatchery steelhead began, 27 March 2007.

I used data from the two river antennas to estimate the proportion of juvenile hatchery steelhead that both emigrated volitionally and exited the study reach prior to the end of the volitional emigration period. I then subtracted this proportion from 1 and multiplied the result by the number of hatchery steelhead that emigrated volitionally- which I obtained by subtracting the number of juvenile hatchery steelhead that emigrated volitionally from the total number released from the 9 raceways as:

$$\hat{S}_2 = \left(1 - \hat{P}_e\right) \times \left(729{,}760 - \hat{S}_1\right), \tag{2}$$

where $\hat{P}_e$ is the proportion of juvenile hatchery steelhead that both emigrated volitionally and exited the study reach prior to the end of the volitional emigration period, and $\hat{S}_2$ is the number of hatchery steelhead that were already present in the study reach on the day sampling of juvenile hatchery steelhead began, 27 March 2007.

I estimated the total number of juvenile hatchery steelhead in the study reach on the day sampling began, defined as:

$$\hat{S}_0 = \hat{S}_1 + \hat{S}_2 , \tag{3}$$

where $\hat{S}_0$ is the total number of juvenile hatchery steelhead in the study reach on the day sampling began, $\hat{S}_1$ is the number of hatchery steelhead that entered the study reach from the hatchery on the day that sampling began and $\hat{S}_2$ is the number of hatchery steelhead that were already present in the study reach on the day sampling of juvenile hatchery steelhead began.

To estimate the number of juvenile hatchery steelhead in the study reach on each day of the study, I regressed the number of unique PIT tag detections (*y*) against the day of study (*x*). Visual inspection of a plot of the data, and trials with various model types, indicated that a power function of the form

$$y = b_0 x^{b_1} \tag{4}$$

best fit the data. I substituted the y-intercept (b_0) in this equation with $\hat{S}_0$, the total number of juvenile hatchery steelhead in the study reach on the day sampling began (obtained from equation 3), with x as the day of study. To obtain the variance for this function in the original units, both the x and y values were $\log_{10}$ transformed. I fit a linear regression of $\log_{10}$ x versus $\log_{10}$ y, to obtain the variance of the regression line. The square root of this variance was exponentiated with a base of 10 and squared to get the variance in original units.

Predation Estimates

I selected an equation developed by He and Wurtsbaugh (1993) that describes the gastric evacuation rate of brown trout that were fed salmonid fry. This equation resulted in a slower rate of gastric evacuation than the equation developed by Elliott (1991), thereby helping to err on the side of underestimating the total number of fry consumed. The equation is given as:

$$\theta_1 \cdot e^{\left(-\theta_2 \cdot T\right)}, \qquad (5)$$

where θ_1 is 56.2 hours, θ_2 is -0.073, and T is water temperature in degrees Celsius. The equation had an R^2 of 0.98.

To calculate a daily fry consumption rate, the amount of hours in a day (24) must be divided by the gastric evacuation rate. To be conservative in the estimate of the total number of fry consumed, I used the number of daylight hours for each day (H_j), which was based on nautical twilight (United States Naval Observatory 2007), instead of 24 hours, because it was not known if piscivorous hatchery steelhead of the Trinity River feed continuously throughout the night. While some salmonids are known to feed continuously throughout the 24 hour period, such as piscivorous coho salmon (Ruggergone 1989), other piscivorous salmonids have been shown to have a diel feeding pattern that is not continuous throughout the 24 hour period (Beauchamp 1990).

Estimates of the proportion of fish that were piscivorous, mean rate of predation by piscivores, and total consumption of salmonid fry were made separately for residualized hatchery steelhead and juvenile hatchery steelhead. The proportion of

piscivorous fish in any given week ($\hat{P}_w$) was estimated by dividing the number of hatchery steelhead that consumed one or more fry in week *w* by the total number of steelhead examined in week *w*. To estimate the total proportion of piscivorous fish throughout the study period, the weekly total numbers of hatchery steelhead that consumed one or more fry were divided by the total number of juvenile steelhead examined. A 95% confidence interval of the proportion (Agresti and Coull 1998, Thompson 2002) of piscivorous fish in any given week was approximated with

$$\hat{P}_w \pm t\sqrt{\frac{\hat{P}_w(1-\hat{P}_w)}{m_w - 1}}\,, \qquad (6)$$

where $\hat{P}_w$ is the estimated proportion of hatchery steelhead that are piscivores from the hatchery steelhead population as a whole during week *w* of the study period, m_w is the total number of steelhead examined during week *w*, and *t* is the upper α / 2 point of the *t*-distribution with m_w-1 degrees of freedom.

For steelhead identified as piscivores, the weekly predation rate ($\bar{y}_w$) was given by

$$\bar{y}_w = \frac{\sum_{i=1}^{n_w} y_{iw}}{n_w}, \qquad (7)$$

where y_{iw} is the number of fry observed in the stomach of fish *i* in week *w*, and n_w is the number of piscivores observed in week *w*, yielding salmonid prey per piscivore. A 95% confidence interval (Thompson 2002) of the mean predation rate was estimated as

$$\bar{y}_w \pm t\sqrt{\frac{\sum_{i=1}^{n_w}\left(y_{iw}-\bar{y}_w\right)^2 \Big/ \left(n_w-1\right)}{n_w}}, \qquad (8)$$

where y_{iw} is the number of fry observed in the stomach of fish *i* in week *w*, and n_w is the number of piscivores observed in week *w* and *t* is the upper α / 2 point of the *t*-distribution with n_w-1 degrees of freedom.

The total number of salmonid fry consumed during the period of study, in the study reach was estimated as:

$$\hat{F} = \sum_{j=1}^{30} \hat{S}_0 \cdot j^{\hat{b}_1} \cdot \frac{H_j}{\theta_1 \cdot e^{(-\theta_2 \cdot T_j)}} \cdot \hat{P}_j \cdot \bar{y}_j, \qquad (9)$$

where $\hat{F}$ is the estimated total fry consumption in the study reach during the study period, $\hat{S}_0$ is the total number of juvenile hatchery steelhead in the study reach on the day sampling began, *j* is the day of study, H_j is the number of daylight hours on the *j*th day (based on nautical twilight), θ_1 is 56.2 hours and θ_2 is -0.073 (see equation 5), T_j is water temperature in degrees Celsius on day *j*, b_1 is the coefficient for the rate of decay of the power function described in equation 4, $\hat{P}_j$ is the estimated proportion of hatchery steelhead that are piscivores from the hatchery steelhead population on day *j*, and $\bar{y}_j$ is the predation rate for steelhead identified as piscivores on day *j*. For the residualized

hatchery steelhead, the same formula was utilized, except the summation was over 21 days.

For $\hat{P}_j$ and $\bar{y}_j$, the weekly values of the piscivore proportion, $\hat{P}_w$, and predation rate, $\bar{y}_w$, were utilized. For example, for any given day in week two of the study, the estimated piscivore proportion and estimated predation rate for week two were used for calculating equation 9. It was assumed that the daily proportion of piscivorous fish and predation rate did not vary within any given week.

Over the five week period during which juvenile hatchery steelhead were studied, 5 days were included in week 1 of the study, 4 days were included in week 5 of study, and 7 days were included in weeks 2-4 yielding 30 days. The timing of the release of hatchery steelhead at the beginning of the study, as well as the timing of water releases from Lewiston Dam at the end of the study, prevented the inclusion of a full 7 days in weeks 1 and 5. Prey consumption of juvenile hatchery steelhead was estimated over a 30 d period and prey consumption of residualized hatchery steelhead was estimated over a 21 d period.

To estimate the number of fry consumed by residualized hatchery steelhead, equation 9 was used, except that $\hat{S}_0 \cdot j^{\hat{b}_1}$ was substituted with the population estimate resulting from the modified Petersen estimator. This population level was held constant for the 21 day residualized hatchery steelhead period of study, assuming no immigration or emigration, and no mortality, natural or otherwise.

To estimate variance of the number of fry consumed by residualized hatchery steelhead and juvenile hatchery steelhead, Gray's (1999) estimator for the variance of a two factor product,

$$\hat{V}(xy) = \bar{x}^2\hat{V}(y) + \hat{V}(x)\bar{y}^2 - \hat{V}(x)\hat{V}(y), \qquad (10)$$

was modified to accommodate constants and a three factor product following Gray (1999). Variance of the total number of fry consumed was estimated assuming daylight hours, temperature, gastric evacuation rate, and survival rate were measured without error. Variances in the proportion of piscivorous fish, predation rate (salmonid fry per piscivore), and population were incorporated into the three factor variance estimator to develop a 95% confidence interval for the number of fry consumed by residualized hatchery steelhead and juvenile hatchery steelhead. Separate estimates of the 95% confidence interval of the number of fry consumed were made for residualized hatchery steelhead and juvenile hatchery steelhead as follows:

$$1.96\sqrt{\sum_{j=1}^{30}\left(\frac{H_j}{\theta_1 \cdot e^{(-\theta_2 \cdot T_j)}}\right)^2 \begin{pmatrix} [\hat{P}_j\bar{y}_j]^2\hat{V}(\hat{S}_j) + \hat{P}_j^{\,2}\hat{V}(\bar{y}_j)\hat{S}_j^{\,2} \\ +\hat{V}(\hat{P}_j)\bar{y}_j^{\,2}\hat{S}_j^{\,2} - \hat{V}(\hat{P}_j)\hat{V}(\bar{y}_j)\hat{S}_j^{\,2} \\ -\hat{P}_j^{\,2}\hat{V}(\bar{y}_j)\hat{V}(\hat{S}_j) - \hat{V}(\hat{P}_j)\bar{y}_j^{\,2}\hat{V}(\hat{S}_j) \\ +\hat{V}(\hat{P}_j)\hat{V}(\bar{y}_j)\hat{V}(\hat{S}_j) \end{pmatrix}} \qquad (11)$$

where H_j is the number of daylight hours on the *j*th day, T_j is the temperature on the *j*th

day, $\frac{H_j}{\theta_1 \cdot e^{(-\theta_2 \cdot T_j)}}$ is the temperature based gastric evacuation rate described in equation 9, $\hat{P}_j$ is the estimated mean proportion of predators on day *j*, $\hat{V}(\hat{P}_j)$ is the estimated variance of proportion of predators on day *j*, $\bar{y}_j$ is the estimated mean predation rate of piscivores, $\hat{V}(\bar{y}_j)$ is the estimated variance of predation rate of piscivores, $\hat{S}_j$ is the estimated mean of either the residualized hatchery steelhead population or the juvenile hatchery steelhead population, and $\hat{V}(\hat{S}_j)$ is the estimated variance of either the residualized hatchery steelhead population or the juvenile hatchery steelhead population.

As in equation 9, for $\hat{P}_j$ and $\bar{y}_j$, the weekly values of the piscivore proportion, $\hat{P}_w$, and predation rate, $\bar{y}_w$, were utilized. I assumed that the daily piscivore proportion and predation rate did not vary within any given week.

For estimation of the number of eggs consumed by residualized hatchery steelhead, I employed the same process used to estimate the number of salmonid fry. I assumed that salmonid fry and salmonid eggs were evacuated from the stomach of piscivorous salmonids at the same rate, although I am not aware of any study that has evaluated the evacuation rate of salmonid eggs from stomachs of salmonids that consume eggs.

Use of equation 11 to estimate the confidence intervals should be regarded as an approximation of confidence intervals. Because PIT tag recovery data collected over the

study period were used to fit a model that was then used to estimate $\hat{S}_0$, $\hat{S}_0$ for the different days are not statistically independent of one another. The expression for estimating variance over time (summations over j = 1 to 30) are likely incorrect because they do not account for covariance among successive estimated values of $\hat{S}_0$. The use of literature based gastric evacuation rates, amount of daylight hours, and water temperature, as constants measured without error, also likely introduces some additional estimate error, but the amount is unknown.

RESULTS

During the course of this study, 315 residualized hatchery steelhead and 1,636 juvenile hatchery steelhead were captured and examined. Of these, 20 (0.95 %) did not have adipose fin clips. One brown trout was also captured during the 3 month duration of study.

Residualized Hatchery Steelhead

A total of 285 residualized steelhead were marked during the period 12 February to 28 February. Snorkelers counted 313 residuals during the resight event on 1 March, of which 38 were marked. Based on these data, I estimate the population of residualized hatchery steelhead in the study reach to be 2,302 (95% CI = 1,681-2,922).

When snorkelers surveyed the reach on 5 February 2007, prior to capture or examination of individual fish, 280 (86%) residualized hatchery steelhead were counted above the large cascade rapid at the Old Weir (rkm 180.7) that lies half way through the study section (Figure 1), while 46 were counted below. On the same date, snorkelers surveyed 3.0 km of the Trinity River downstream of the end of the study area, and counted seven residualized hatchery steelhead.

The 315 residualized hatchery steelhead examined during this study averaged 331 mm in length (SD = 51 mm; range = 243-494 mm), and 408.4 g in weight (SD = 215.2 g; range = 148.7-1415.8 g) (Table 2). Of the residuals examined, 90 % were smaller than 420 mm, which is the cut-off in fork length below which steelhead are considered to

Table 2. Age composition for 98 residualized hatchery steelhead from the upper-Trinity River, California.

	Age		
	2	3	>3
Sample size	54	33	11
Mean fork length (mm)	310	383	459
Mean weight (g)	328.5	614.0	1001.3

exhibit a half-pounder life-history by CDFG (California Department of Fish and Game 2005). There were 29 fish (9%) that were considered to be transitional or smolting. Mean fork length was greater for non-smolting individuals (mean = 333 mm) than for transitional or smolting individuals (mean = 306 mm) (*t*-test, $t = 4.38$; df = 48; $P < 0.001$).

Scale samples of residualized steelhead were collected to evaluate the duration of residualism in the upper Trinity River, and to inspect for evidence of anadromy. Of 99 samples collected, one came from an individual that was 427 mm in length and showed signs of ocean entry and ocean growth. Of the remaining scales, 54 were collected from individuals that were 2 years old, 33 were from individuals aged at 3 years old, and 11 were from fish older than 3 years of age (Table 2). Mean fork length was larger for individuals that were aged (mean = 351 mm) than for individuals that were not aged (mean = 320) (*t*-test, $t = 4.82$; df = 139; $P < 0.001$). This suggests that residualized steelhead that were aged may not be entirely representative of the population as a whole. Ocean growth was clearly evident in the anadromous hatchery steelhead scales. In the residualized hatchery steelhead scales, the spacing of circuli was much tighter and more consistent than that of anadromous hatchery steelhead (Figure 2). Growth in the hatchery was also evident in most residualized steelhead samples, with circuli in the first year of life spaced noticeably greater than in successive years (Figure 2).

Hatchery steelhead residuals were generally smaller than their anadromous counterparts and typically more football shaped than the streamlined anadromous hatchery steelhead. Body morphology, in combination with more colorful fins, a more

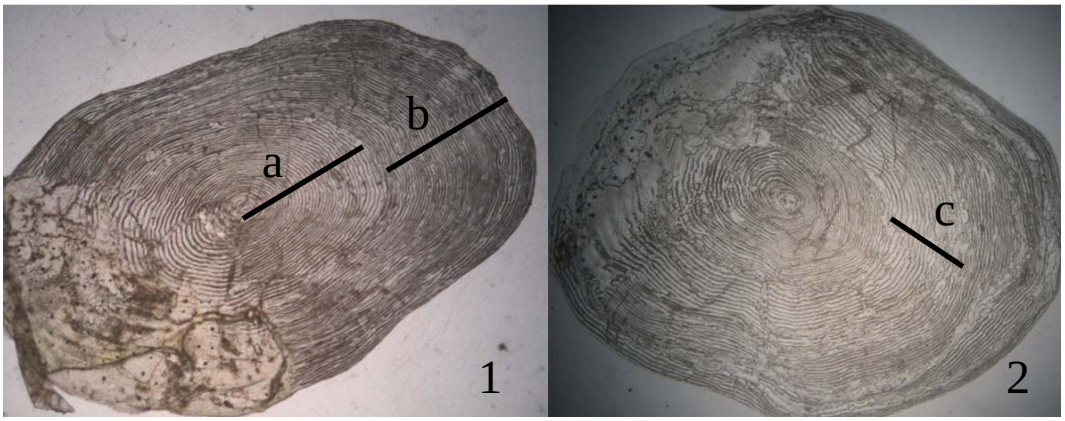

Figure 2. Images of hatchery steelhead scales from the upper-Trinity River, California, 2007. From left to right: 1) a residualized hatchery steelhead >3 years old (468 mm in length) showing wide spacing of first 30-35 circuli from 1 year of robust hatchery growth (a), followed by tightly spaced and uniform circuli from several years of river growth (b) and; 2) an anadromous hatchery steelhead (635 mm in length) showing several signs of anadromy including ocean growth (c) with wider spacing of circuli than that of the first 30-35 circuli of hatchery growth, as well as ocean entry/exit markings.

vibrant pink stripe on the body, and spotting dissimilar to anadromous steelhead, gave the residuals a “troutlike” appearance. Many residuals, including some as small as 285 mm, were observed to be in full spawning colors. Several were ripe males that excreted milt upon examination. I often observed residuals positioned behind spawning anadromous steelhead.

Juvenile Hatchery Steelhead

Of the 1,636 juvenile hatchery steelhead captured during this study, 771 were captured below the Old Weir Hole, located half way through the study reach, while 865 were captured above it (Table 3). Average fork length and weight for juvenile hatchery steelhead was 167 mm (SD = 29 mm; range = 84-249 mm) and 54.6 g (SD = 30.6 g; range = 6.8-217 g), respectively (Table 4). The fork length of juvenile hatchery steelhead differed among smolting categories (not-smolting, transitional, and smolting) (ANOVA; $F = 107.12$; df = 1,554; $P < 0.001$). Multiple comparisons showed each group was significantly different from the other (Tukey’s 95% Simultaneous Confidence Intervals = 98.06%). Individuals that were not smolting (mean fork length = 159 mm; SD = 31 mm; range = 84-249 mm) were the smallest group, followed by transitional fish (176 mm; SD = 20 mm; range = 125-240 mm), with smolting fish having the largest average fork length (186 mm, SD = 17 mm, range = 154-240 mm). Condition factors also differed among groups (ANOVA; $F = 113.5$; df = 1,554; $P < 0.001$). Multiple comparisons showed each group was significantly different from the other

Table 3. Sampling locations, method of capture, and sample size of juvenile hatchery steelhead captured at each location in the upper Trinity River, California, in March of 2007.

Location	rkm	Electrofishing	Hook and line	Seine	Total
Old bridge	179.2	0	272	163	435
Cableway	179.5	0	44	0	44
New bridge	180.4	0	169	0	169
Corner	180.5	0	123	0	123
Weir	180.7	0	256	0	256
Sven Oldertson	181.1	58	0	0	58
Bear Island	181.4	151	247	0	398
Three pipes	181.9	0	72	0	72
First Riffle	182.2	0	81	0	81

Table 4. Fork length, weight, and fry consumption of non-smolting, transitional, and smolting juvenile hatchery steelhead captured in the upper-Trinity River, California 2007, using hook and line, seine, and electroshocker.

	Areas other than Bear Island				Bear Island only[a]				
	Juvenile category				Juvenile category				
Variable	Non-smolting	Transitional	Smolting	Sub-total or mean	Non-smolting	Transitional	Smolting	Sub-total or mean	Grand total or mean
Sample size	696	419	123	1,238	295	92	11	398	1,636
Mean fork length (mm)	156	175	186	166	169	184	199	173	167
Mean weight (g)	43.8	57.6	66.0	50.9	63.5	67.8	83.8	65.0	54.6
Piscivores (*n*)	45	28	9	82	120	17	2	139	221
Piscivore proportion	0.06	0.07	0.07	0.07	0.41	0.18	0.18	0.35	0.14
Fry consumed	65	32	12	109	715	53	5	773	882
Fry per piscivore	1.4	1.1	1.3	1.3	6.0	3.1	2.5	5.6	4.0

[a] The data are given for one location called Bear Island and the rest of the river separately, due to the high rate of salmonid fry consumption by juvenile hatchery steelhead at the Bear Island site.

(Tukey's 95% Simultaneous Confidence Intervals = 98.06%). Mean condition factor of individuals that were not smolting was the highest (1.11) followed by fish that were transitional (1.05), with smolting individuals having the lowest condition factor (1.01).

Mean fork length and weight for 500 (50 from each of 10 raceways) juvenile hatchery steelhead examined in the hatchery on 14 March 2007, one day prior to the beginning of the volitional release period, were 178 mm (SD = 34 mm; range = 62-246 mm) and 76.2 g (SD = 34.4 g; range = 2.1-188.1 g), respectively. Overall, the difference in fork length between 108 juvenile hatchery steelhead captured by hook and line during the first week of study (mean = 182 mm; SD = 27 mm; range = 121-242 mm) and that of the 500 juvenile hatchery steelhead examined one day prior to the beginning of the volitional release period was not significant (*t*-test; $t = 1.29$, df = 184, $P = 0.198$).

Mean fork length and weight of juvenile hatchery steelhead captured by seining and electrofishing in the river ($n = 371$) were 162 mm (SD = 31 mm, range = 95-248 mm) and 52.2 g (SD = 34.0 g, range = 10.4-217.5 g), respectively. For juvenile hatchery steelhead captured by hook and line on the same dates and locations as those captured by seining and electrofishing ($n = 317$), mean fork length and weight were 166 mm (SD = 27 mm, range = 100-249 mm) and 52.9 g (SD = 29.3 g, range = 13.4-198.0 g), respectively. Fork length of juvenile hatchery steelhead captured within the river differed between capture methods (*t*-test, $t = 2.18$, df = 685, $P = 0.030$). However, it is unknown if these differences, which appear to be small, are biologically meaningful.

PIT-tag antenna performance and juvenile hatchery steelhead population estimation

The read range and efficiency of PIT-tag antennas was greater in the hatchery than in the river. Hatchery antennas had a read range of approximately 102 cm, and tests indicated an efficiency close to 100% with that read range. Of 991 PIT tags that were implanted in the juvenile hatchery steelhead 6 weeks prior to the beginning of the volitional release period, 877 (88%) were subsequently detected by the hatchery array (Figure 3). Of these, 859 (98%) were detected on both hatchery antennas. Given the high detection efficiency, undetected tags likely reflected either rejection by the fish, or fish mortality prior to release.

Read range of the river antennas was roughly 25 cm, and their efficiency ranged between 65% and 80% throughout the study. Measuring efficiency of the river antennas accurately was difficult with test tags because the orientation of the test tags could not always be controlled, which can greatly affect antenna performance (Zydlewski et al. 2006). Of 877 tagged juvenile steelhead that were detected leaving the hatchery, 663 were detected with the river array, with an overall efficiency of at least 76% (Figure 4). Some of the tagged fish that were detected in the hatchery may have residualized upstream of the river array, or died before reaching it.

The river array was not operational until 19 March, 4 days after the volitional release period began. During this four day period, 33 PIT-tagged steelhead exited the hatchery, 9 of which were eventually detected at the river array.

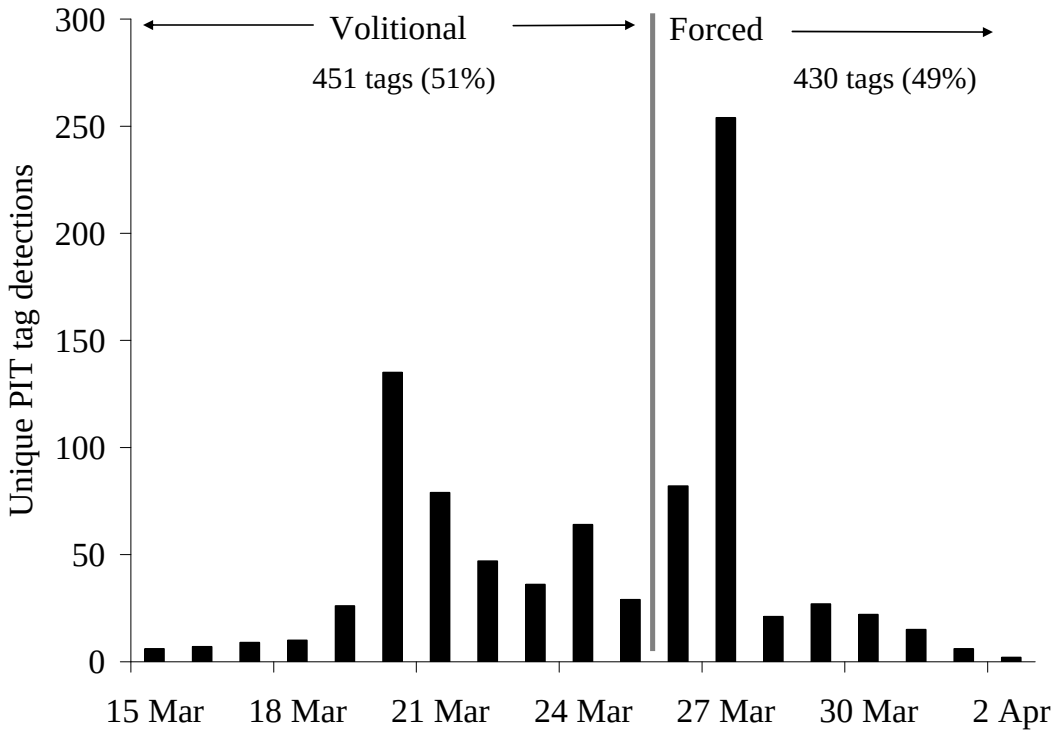

Figure 3. The number of unique detections (first date a tag was detected) of PIT-tagged juvenile steelhead by day, for an array of 2 antennas located in Trinity River Hatchery Juvenile steelhead were forced from the hatchery on 26 and 27 March 2007 following an 11 day volitional emigration period.

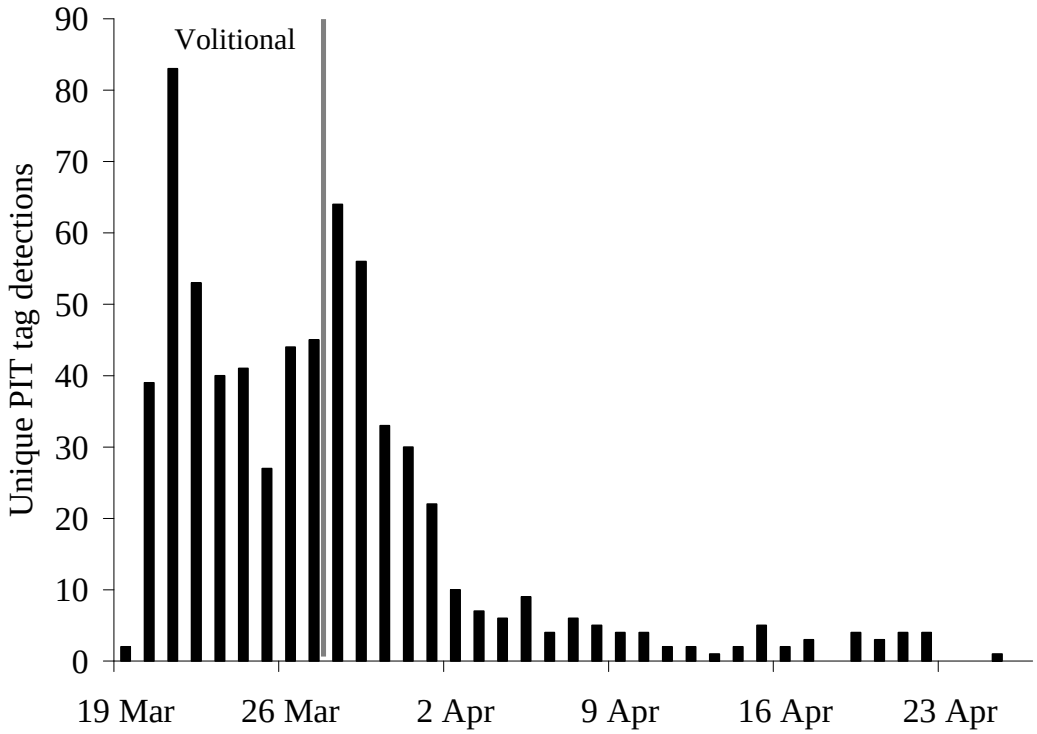

Figure 4. The number of unique detections (first date a tag was detected) of an array of 2 antennas located 3.2 km downstream in the Trinity River (right). Juvenile steelhead were forced from the hatchery on 26 and 27 March 2007 following an 11 day volitional emigration period.

The supporting cable of the downstream river antenna broke on 11 April and was not repaired. During the time that two antennas were in operation, 564 tagged fish were detected. Of these, 276 (49%) were detected at both antennas, while 288 (51%) were detected at only one of the two antennas. Downstream and upstream river antennas appeared to perform similarly. Of the 288 tags detected on one of two antennas, 156 were detected on the upstream antenna and 132 were detected on the downstream antenna.

An estimated 356,975 juvenile hatchery steelhead failed to migrate volitionally from the hatchery. These fish entered the river at the end of the volitional release period, at which time sampling of juvenile steelhead in the river began. A total of 823,210 juvenile hatchery steelhead were released from Trinity River Hathcery between 15 to 27 March 2007. The number of juvenile hatchery steelhead released from 9 raceways that contained PIT-tagged fish was 729,760. Fifty-one percent (n = 448) of tagged fish exited the hatchery volitionally (Figure 3). Remaining fish (P_f = 0.49) were forced from the hatchery by dewatering of raceways by hatchery personnel.

Prior to 27 March 2007, the end of the volitional release period, 326 of 448 juvenile steelhead that were detected leaving the hatchery were also detected by the river array (Figure 4). This suggests that at least 73 % (P_e) of volitional migrants exited the study reach prior to collection of stomach contents of juvenile steelhead. Multiplying the number of juvenile hatchery steelhead that migrated volitionally by 0.27 (1-0.73) yielded a product of 100,488 fish ($\hat{S}_2$). The number of juvenile hatchery steelhead that failed to migrate volitionally and entered the river on the day sampling commenced was estimated

to be 357,582 ($\hat{S}_1$). The total number of juvenile hatchery steelhead present in the study reach on 27 March ($\hat{S}_0$) was estimated as the sum of $\hat{S}_1$ and $\hat{S}_2$. An estimated 458,070 ($\hat{S}_0$) juvenile hatchery steelhead were present in the study reach on 27 March 2007.

To estimate the number of juvenile hatchery steelhead present in the study reach during each day of the study, the number of unique tag detections (first date and time a particular tag was detected) from the river array was regressed over time. Examination of a plot of the data, and trials with various model types, indicated that a power function of the form $y = b_0 x^{b_1}$ provided the best fit (r^2 = 0.89). The equation was:

$$y = 73.44\, j^{-0.92}, \qquad (12)$$

where j is the number of days beyond 27 March 2007. The value for b_0 was substituted with 438,304, the number of hatchery steelhead that were estimated to be in the study reach on 27 March. Model results suggest that the hatchery steelhead population decreased sharply in the beginning of the study, losing roughly half of the total population within the first 24 hours (Figure 5).

Fry consumption

Consumption of salmonid fry varied among juvenile hatchery steelhead. The smallest piscivorous hatchery steelhead had a fork length of 108 mm, and it consumed 2 salmonid fry. A juvenile hatchery steelhead that was 200 mm in length consumed 52 salmonid fry, which was the maximum amount of salmonid fry consumed by any

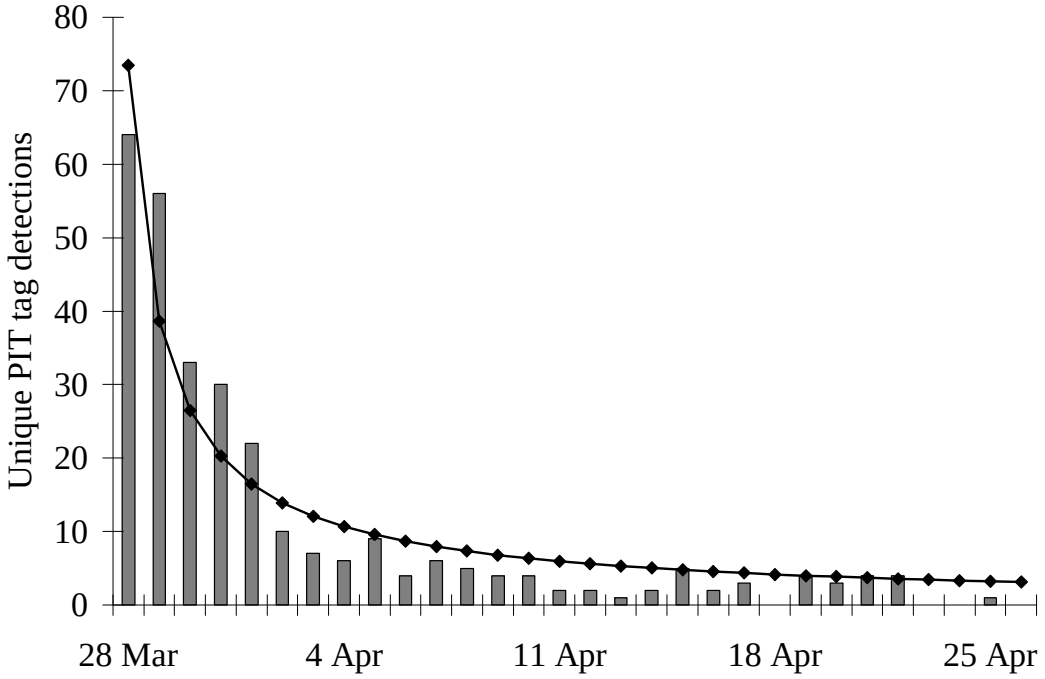

Figure 5. The number of unique detections (first date a tag was detected) of PIT-tagged juvenile steelhead, by day, for an array of 2 antennas located in the Trinity River, California, 2007, 3.2 km downstream from the release site, and a regression of the data with a power function. The data were fit to a power function as $y = 73.44x^{-0.923}$, $R^2 = 0.89$.

hatchery steelhead during this study. Eighty-one of 316 residualized hatchery steelhead (26%) consumed a total of 435 salmonid fry. Additionally, 97 residualized steelhead consumed a total of 2,685 salmonid eggs. The maximum number of salmonid fry consumed by any residualized steelhead was 35, while the maximum number of eggs consumed by any one residualized steelhead was 162. The proportion of piscivores in the residualized steelhead population ranged between 0.20 and just over 0.30 (Figure 6). The number of fry consumed per piscivore decreased from a high of around eight in the first week of study, to roughly 4 in the last week of the study (Figure 6). The average fork length of residualized hatchery steelhead piscivores (363 mm; SD = 61 mm) was greater than that of non-piscivores (319 mm; SD = 41 mm) (*t*-test, $t = 6.08$, df = 104, $P < 0.001$).

Of 1,636 juveniles examined, 221 piscivores (13.5 %) consumed 882 salmonid fry (Table 4). The proportion of piscivores in the juvenile steelhead population increased from about 0.02 in the beginning of the study to about 0.1, before falling back down to around 0.04 by the end of the study (Figure 7). Excluding those hatchery steelhead captured at Bear Island, the amount of fry consumed per piscivore remained consistent between weeks, slightly greater than 1.0 (Figure 7). The average fork length of juvenile hatchery steelhead piscivores (173 mm, SD = 28 mm) was greater than that of non-piscivores (168 mm, SD = 29 mm) (*t*-test, $t = 2.85$, df = 295, $P = 0.005$). The differences between the proportion of piscivores and the number of fry consumed per piscivore for the three smoltification groups were small (Table 4).

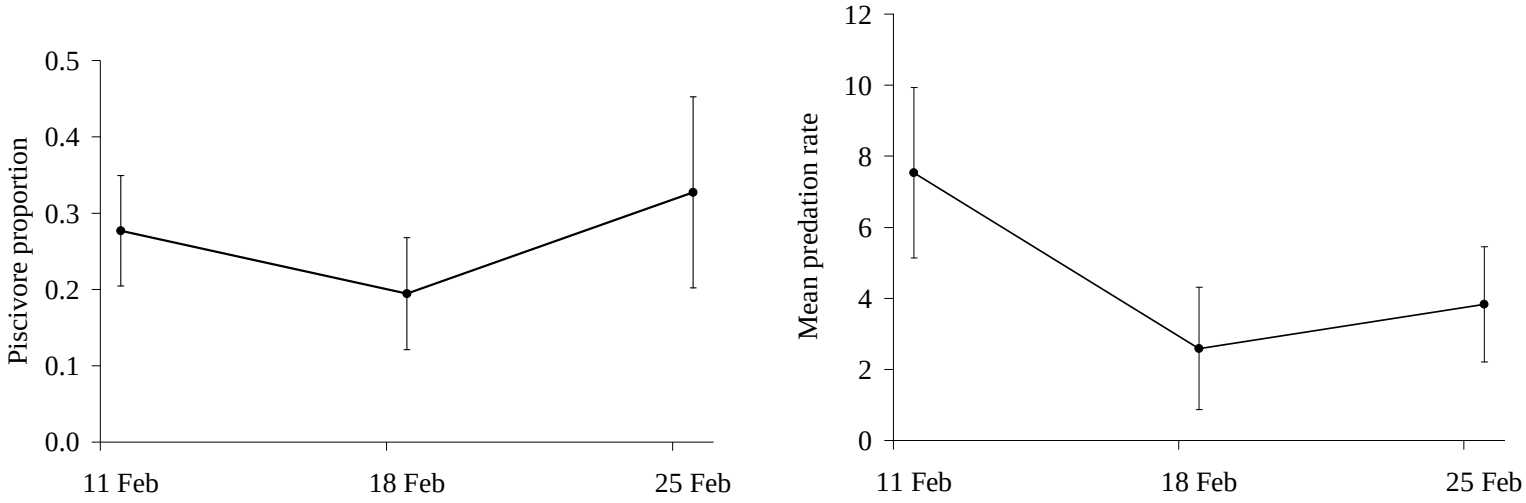

Figure 6. The proportion of piscivores (piscivores/ number of fish examined) ± 95% CI and the mean rate of predation (number of salmonid fry/piscivore) ± 95% CI for residualized hatchery steelhead captured from the upper Trinity River, California, 2007.

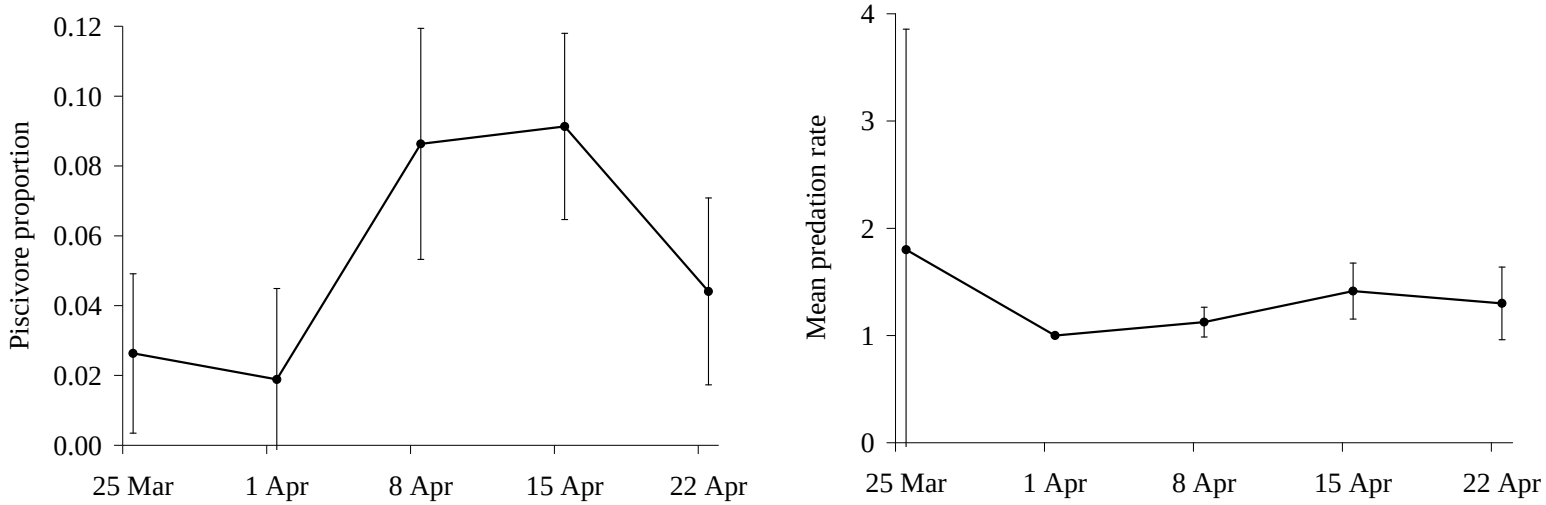

Figure 7. The proportion of piscivores (piscivores/ number of fish examined) ± 95% CI and the mean rate of predation (number of salmonid fry/piscivore) ± 95% CI for juvenile hatchery steelhead captured from the upper-Trinity River, California, 2007. The juvenile data excludes those fish captured at Bear Island.

Two years earlier, 2,479 juvenile salmonids consumed 135 salmonid fry in the same study reach (Yurok Tribal Fisheries Program 2008). Differences in fry consumption between the two years likely arises from a single sampling location, a side channel at Bear Island (rkm 180.4), which was sampled in 2007, but not 2005.

The observed count of piscivores between the juveniles captured at Bear Island and those not captured at Bear Island (Table 4) differed from the expected count (χ^2 = 140.897, $P < 0.001$). Likewise the amount of fry consumed per piscivore between the two groups differed from the expected count (χ^2 = 75.581, $P < 0.001$). Prior to this study, the initial investigation of predation rates by hatchery steelhead had not uncovered the high rate of predation that was recorded at Bear Island.

Samples obtained by seining and electrofishing were compared with samples obtained by hook and line on the same dates and in the same locations (4 different occasions in total). Of 372 juvenile hatchery steelhead captured by seine and electrofishing, 100 piscivores consumed a total of 635 salmonid fry. Of 317 juvenile hatchery steelhead captured by hook and line, 62 fish consumed 159 salmonid fry. Fish sampled by seining and electrofishing consumed 6.4 salmonid fry per piscivore, while fish sampled by hook and line consumed 2.6 fry per piscivore. The proportion of piscivorous hatchery steelhead did not differ with capture technique (seining/electrofishing versus hook and line) (χ^2 = 3.179, P = 0.075), but the number of fry consumed per piscivore did (χ^2 = 25.204, $P < 0.001$).

I estimate that 24,194 [21,066-27,323] salmonid fry were consumed by 2,302 residualized hatchery steelhead in 21 days from 10 February to 2 March 2007.

Additionally, I estimate that the residualized hatchery steelhead consumed 171,018 [155,272-186,764] salmonid eggs during the same period. Assuming an egg-to-fry survival rate of 0.25, the 171,018 eggs consumed by the residualized hatchery steelhead would equate to 42,755 salmonid fry.

Excluding results from the Bear Island side channel, I estimate that 437,697 juvenile hatchery steelhead consumed 61,214 [43,813-78,615] salmonid fry in 30 days from 28 March to 26 April 2007. Assuming a constant population of 1,500 juvenile hatchery steelhead in the Bear Island side channel in the 30 day period, an additional 49,445 salmonid fry were consumed.

DISCUSSION

This study documents the highest rate of predation by hatchery salmonids on naturally produced salmonids that has been reported (Table 1). Some attributes of the upper Trinity River setting contribute to high predation risk for naturally produced salmonid fry. These include spatial and temporal overlap of predator and prey (Hatchery Scientific Review Group 2004), size differential of predator and prey (Pearsons and Fritts 1999), high concentrations of predators (Mather 1998), as well as abiotic factors including low, regulated flow (8.5 ms^{-1}) and high water clarity (< 2 NTU; Gregory and Levings 1998, Robertis et al. 2003). Because salmonids are visual predators, another factor controlling the encounter rate of prey is prey density (Beauchamp et al. 1999). The study area is heavily used by spawning adult salmonids, resulting in high concentrations of prey, relative to other parts of the river with lower redd densities.

The release of large numbers of hatchery steelhead can lead to substantial numbers of fry being consumed, even with relatively low predation rates. For example, if 500,000 hatchery steelhead are released, and 5% of these hatchery steelhead consume 1 fry per day, then 25,000 fry can be consumed in one day. The amount of fry consumed is additive, with hatchery steelhead continuing to consume fry each successive day.

The majority of salmonid spawning in the uppermost 40 km of the Trinity River (California Department of Fish and Game 2005) takes place within 3.2 km of the release location of hatchery juvenile salmonids, so that both predator and prey exist in close

proximity to each other. In 2006, there were an estimated 2,302 redds for Chinook salmon and coho salmon combined, although some coho salmon and Chinook salmon may have spawned after redd surveys were terminated on 16 December 2006. Assuming 3,000 eggs per redd and an egg-to-fry survival rate of 0.25, approximately 1,726,500 salmon fry were produced in the study reach. Assuming all fry consumed by hatchery steelhead were Chinook salmon or coho salmon fry, half of the eggs consumed by residualized steelhead were Chinook salmon or coho salmon (the other half being steelhead), and an egg-to-fry survival rate of 0.25, then I estimate that 156,231 Chinook salmon and coho salmon fry were consumed over the 21 d residualized hatchery steelhead study period and the 30 d juvenile hatchery steelhead study period. This represents 9.0 % of Chinook salmon and coho salmon fry that were produced.

For several reasons, the estimate above is not a complete estimate of the number of fry consumed by hatchery steelhead in 2007. The estimate covers only the 21 d and the 30 d periods of study for residualized hatchery steelhead and juvenile hatchery steelhead, respectively. Additionally, almost half of the juvenile hatchery steelhead produced at Trinity River Hatchery in 2007 were not included in this study. The study reach was only a 3.2 km long, the fly only hook and line method utilized may lead to underestimation of fry consumption, and the study only covered a relatively short portion of the entire year. Also, dividing the number of daylight hours by the temperature-based gastric evacuation rate of steelhead resulted in a “correction” of the fry consumption data by approximately one-half throughout the study. Trinity River Hatchery also releases roughly 500,000 coho salmon annually that were not included in this study. Coho salmon

have also been documented to consume salmonid fry (Ruggergone and Rogers 1992, McConnaughey 1999).

I found that the average fork length of juvenile hatchery steelhead piscivores was greater than that of non-piscivores. However the difference was five mm, which, while statistically significant, may not be biologically significant. Because the difference between these two groups was relatively small, and the fact that a wide range of juvenile steelhead size classes consumed salmonid fry, it is unlikely that there is a size at which juvenile hatchery steelhead can be released that would reduce the probability that they would consume salmonid fry. The differences between the proportion of piscivores and the number of fry consumed per piscivore for the three smoltification groups were small (Table 4). This indicates that hatchery rearing strategies aimed at increasing the number of steelhead that are ready to smolt upon release may not affect the number of fry consumed by hatchery steelhead. However, because non-smolting hatchery steelhead are more likely to residualize, non-smolting hatchery steelhead may consume more salmonid fry simply because they spend more time in the river than those that are capable of smolting when released.

Both juvenile hatchery steelhead and juvenile coho salmon are released on 15 March of each year. March is a time of year when many fry are either newly emerged, or just emerging from the gravel (Trinity River Flow Evaluation 1999), making the fry susceptible to predation. Residualized hatchery steelhead are present throughout the months that all salmonids spawn and rear. This study has shown that residualized steelhead take advantage of both fry and eggs in the drift, as well as actively pursuing

rearing fry. For instance, I saw hundreds of adult steelhead spawning in February in areas where Chinook salmon and coho salmon had already spawned (redd superimposition). Spawning adult hatchery steelhead, upon creating their own nests, would excavate the yolk sac fry and eyed eggs of salmon, sending them into the water column, making for a readily available food resource for residualized hatchery steelhead.

Data from a comparison of fish samples collected by hook and line and those captured by other means suggests that hook and line may underestimate the number of salmonid fry consumed. This indicates that by relying on invertebrate fly patterns to attract juvenile hatchery steelhead, I may have failed to capture those juveniles that specialize in piscivory. For instance, if one casts a floating insect to a group of juvenile hatchery steelhead, an individual that typically focuses on pursuing salmonid fry may be less likely to be the first to look up and strike the dry fly than an individual that focuses on preying upon insects. I often witnessed juvenile hatchery steelhead pursuing salmonid fry in the shallows along the stream banks. It became clear after spending hours watching individual steelhead rush into groups of fry, that some hatchery steelhead tend to specialize in the pursuit of fry, while others do not. This has implication for the results of this research because the majority of the samples (77%) were captured using hook and line with invertebrate fly patterns, possibly underestimating the number of fry consumed.

Undoubtedly, several of the juvenile hatchery steelhead in raceway F, the only raceway that was not included in this study or in the calculations of fry consumption, were larger in size than the smallest piscivore that was recorded during this investigation, and therefore capable of consuming salmonid fry. This means that it is possible that

some juvenile hatchery steelhead from raceway F, which on average contained the smallest steelhead released from Trinity River Hatchery, also consumed salmonid fry, thereby underestimating of the total number of fry consumed during the period of study in the study reach. In total, 384,906 juvenile hatchery steelhead were not included in the calculation of the number of fry consumed.

The relatively high rate of predation by juvenile hatchery steelhead on naturally produced fry at the Bear Island side channel was suprising. The number of fry per piscivore at Bear Island was roughly four times that of the rest of the study site (Table 4). Previous sampling by the Yurok Tribal Fisheries Program did not reveal large variation in predation rates at various locations throughout the study reach, but their survey did not sample juvenile hatchery steelhead at the Bear Island site. High predation may reflect a higher concentration of fry per unit of volume than in other areas of the river, and (or) it could reflect learned behavior by hatchery fish. Several juvenile hatchery steelhead had both feed pellets and invertebrates in their stomachs on the first day of our study, indicating that they quickly begin feeding on insects and other food particles in the drift.

Length of juvenile hatchery steelhead in my study was considerably smaller than in the survey conducted by the Yurok Tribal Fisheries Program in 2005 (Yurok Tribal Fisheries Program 2008). Average length differed by 30% (214 mm versus 167 mm) between the two studies. The study by the Yurok Tribal Fisheries Program (2008) found that 78% of juvenile hatchery steelhead examined were transitional or smolting. In this study, only 39% of juvenile hatchery steelhead were transitional or smolting. This is evidence that the average difference of 47 mm in fork length between juvenile steelhead

captured in 2005, and those captured in 2007, is not only statistically significant, it is also biologically meaningful. Variability in release size affects inferences regarding survival and adult returns because both survival (Tipping 1997, Miyakoshi et al. 2001, Jokikokko et al. 2006) and smoltification, to a point (Chrisp and Bjornn 1978, Tipping et al. 1995), are positively correlated with juvenile size. Annual variability in release size of juvenile steelhead from Trinity River Hathcery may reflect variability in air temperature, weather, and water temperature, as fish are reared in outdoor raceways.

Chrisp and Bjornn (1978) determined that steelhead parr must reach a minimum total length of 140-160 mm before they have the capability to become smolts and migrate to the sea. Those that were greater than 170 mm in length had more pronounced changes associated with smoltification, and migrated in larger numbers, than smaller juveniles. Rhine et al. (2002) found that steelhead classified as smolts were significantly longer, heavier, and had lower mean condition factor than steelhead classified as transitional or not smolting. This agrees with my findings. Additionally, larger smolt size has been linked with increased rates of survival (Ward and Slaney 1988, Henderson and Cass 1991, Tipping 1997, Miyakoshi et al. 2001, Jokikokko et al. 2006), especially in years with poor ocean conditions (Saloniemia et al. 2004). However, the positive correlation between steelhead smolt size and percentage migrating (Chrisp and Bjornn 1978, Tipping et al. 1995) and survival (Tipping 1997) tends to disappear at roughly 190-210 mm, after which point residualism and precocialism begin to increase (Schmidt and House 1979, Partridge 1986, Viola and Schuck 1995, Newman 2002, Rhine et al. 2002). Tipping et al. (1995) reported that for optimum emigration rates, steelhead smolt lengths should be at

least 190 mm and that Fulton's K values should be 0.90-0.99. Excessively large smolts conferred no clear emigration advantage, and were costlier to produce. However, average fork length should exceed 190 mm, in order to account for the normal distribution of a population (Tipping et al. 1995, Tipping 1997).

Because they are not, on average, physiologically capable of smolting, the 175,210 juvenile hatchery steelhead in raceways F (mean fork length = 125 mm) and N (mean fork length = 128 mm) of Trinity River Hatchery were forced into one of two probable pathways which are both undesirable from a management perspective: death or residualism. As mentioned above, mortality tends to be highest for smaller steelhead smolts (Seelbach 1987, Ward and Slaney 1988). Those that do survive compete with naturally produced salmonids for food and habitat (McMichael et al. 1997), exhibit aggression toward other salmonids (Berejikian et al. 1996, McMichael et al. 1999), and consume other salmonids (this study).

Although estimates of the number of residualized steelhead that exist in the upper Trinity River during summer months are not available, tens of thousands may persist throughout the summer (in any given year). Researchers have estimated residualism rates of 10-17% on other river systems (Viola and Schuck 1995, Rhine et al. 2002, Bumgarner et al. 2002). Snorkel surveys in June from previous years have documented tens of thousands of juvenile hatchery steelhead in the upper Trinity River (personal communication, P. Garrison, 2007 California Department of Fish and Game, P.O. Box 1185, Weaverville, CA 96093). For example, Bumgarner (2002) estimated that the number of residualized steelhead present in the Touchet River on 27 May 1999 was

18,411, or 14.7% of the 125,000 released. Assuming a minimum of 10% of steelhead from Trinity River Hatchery fail to migrate by 1 June, roughly 80,000 hatchery steelhead could be present in the Trinity River, most likely in the uppermost reaches.

In two separate years (2005 and 2007) only a few thousand fish were estimated to persist into March from releases of roughly 800,000 the previous year (Yurok Tribal Fisheries Program 2008, this study). The fate of the large number of steelhead that likely remain in the Trinity River between the time of release and the spring of the following year is not known. Most of the fish probably perish, as non-migratory juvenile steelhead tend to have high rates of mortality in freshwater (Chrisp and Bjornn 1978, Seelbach 1987), although some probably continue to smolt throughout the summer months. For example, Chrisp and Bjornn (1978) found that for yearlings planted in the spring, high mortalities (70%) occurred the following summer. It is not advantageous, from a management perspective, for juvenile hatchery steelhead to remain in the river for one year after release, and then migrate to the ocean, because they interact with naturally produced salmonids in the river (McMichael et al. 1997, McMichael et al. 1999, Kostow et al. 2003) and they have low survival rates (Chrisp and Bjornn 1978, Seelbach 1987).

Overall mean fork length for juvenile hatchery steelhead that were captured during the first week of this study was not significantly different from the mean for the 500 juvenile hatchery steelhead that were measured one day prior to release from the hatchery. This indicates that the hook and line method provided a reasonable means to sample fish without bias in relation to fish size. Because longer steelhead, up to roughly 200 mm, smolt at a greater frequency than smaller steelhead (Chrisp and Bjornn 1978,

Rhine et al. 2002), it is possible that longer fish continually exited the study reach throughout the course of the investigation, making the mean fork length decrease over time. For instance, the mean length of fish captured during the first week of the study was 182 mm, while the overall mean for the duration of the study was 167 mm.

Even though Trinity River Hatchery serves as one of the large mitigation hatcheries in California, fishing regulations on the uppermost 3.2 km of the Trinity River are “fly only” and “catch and release only”. These regulations have no apparent biological justification. Fish and game agencies in some western states rely on angler harvest to eliminate residualized hatchery steelhead (Partridge 1985). Without this tool, river managers have few available means to eradicate non-anadromous steelhead from the river. Catch and release regulations that are, in this case, closely associated with a large hatchery, may obscure the overall purpose and ethic of catch and release angling from the fishing public, which is meant to preserve wild fish. The California Fish and Game Commission Policy (2004) states that

> “Resident fish will not be planted or resident fisheries developed in drainages of salmon [or steelhead] waters, where, in the opinion of the Department, such planting or development will interfere with salmon [or steelhead] populations. Exceptions to this policy may be authorized by the Commission (a) where the stream is no longer adaptable to anadromous runs, or (b) during the mid-summer period in those individual streams considered on a water-by-water

> basis where there is a high demand for angling recreation and such planting or development has been determined by the Department not to be detrimental to salmon [or steelhead]."

A fishery for non-anadromous hatchery steelhead now exists on the Trinity River. These residualized fish cannot legally be removed by anglers; however, they are targeted by fly fishermen. To date, the California Department of Fish and Game has not examined whether or not this resident fishery is detrimental to salmon or steelhead. Without this information, it is not possible to determine if the fishery is in conflict with the stated policies of the California Fish and Game Commission. Additionally, in some years, tens of thousands of adult hatchery salmonids, in excess of hatchery egg take goals, are returned to the river after entering the hatchery, and they cannot be harvested.

During the course of this study, I learned that virtually 100% of the steelhead broodstock at Trinity River Hatchery is of hatchery origin (personal communication, L. Marshall, 2007, California Department of Fish and Game, 1000 Hatchery Rd., Lewiston, CA 96052). Hatchery-reared, adipose fin clipped anadromous steelhead have been bred at Trinity River Hatchery for decades, with little, if any, genetic input from naturally produced steelhead. In order for the selection regimes in the natural environment to dominate the mean fitness of the hatchery and naturally produced population as a whole, it is recommended that the proportion of hatchery broodstock composed of naturally produced fish must exceed the proportion of hatchery fish spawning in the river (Hatchery Scientific Review Group 2004). For example, if the hatchery uses 10%

naturally produced steelhead for broodstock, then only 10% of steelhead that spawn naturally should be of hatchery origin so that the hatchery does not produce deleterious changes in the hatchery and naturally produced populations. Since Trinity River Hatchery uses virtually 100% hatchery steelhead broodstock, and the percentage of naturally spawning adults in any given year is roughly 75% (Trinity River Flow Evaluation 1999, California Department of Fish and Game 2005), the hatchery, and not the Trinity River, may be driving the natural selection process. This means that steelhead in the upper Trinity River mainstem might be better adapted to reproduction in the hatchery than in the Trinity River. This has bearing on this study and on the restoration of naturally produced fish in the Trinity River. This is because hatchery programs have the potential to significantly alter the genetic composition (Crozier 1998, Lynch and O'Hely 2001, Saisa et al. 2003), phenotypic traits (Einum and Flemming 1997, Hard et al 2000, Kostow 2004, Wessel et al. 2006), behavior (Mesa 1991, Berejikian et al. 1996, Fleming et al. 1996, Jonsson 1997), survival (Jonnnson et al. 2003, McGinnity et al. 2003, Kostow 2004) and ultimately the reproductive success (Reisenbichler and Rubin 1999, Fleming et al. 2000, Mclean et al 2003, Araki et al. 2007) of anadromous salmonids, potentially in a matter of a few generations (Araki et al. 2007). Egg transfers from Iron Gate Hatchery to Trinity River Hatchery were routine until at least 1994, and hatchery steelhead of the Trinity River are more genetically similar to Klamath River steelhead than they are to wild steelhead from Horse Linto Creek, a tributary to the Trinity River (Pearse et al. 2007).

While I did not study the effects of competition between hatchery and naturally produced salmonids in the river, others have reported negative impacts on naturally produced salmonids (Kennedy and Strange 1986, McMichael et al. 1997, McMichael et al. 1999), even to the point of measurably impacting the population of natural salmonids (Kostow et al. 2003, Kostow and Zhou 2006). Competition between hatchery and naturally produced salmonids may be more harmful than predation by hatchery salmonids on naturally produced salmonids, but its effects can be less visible. The end result of the competition may be dead naturally produced fish, which cannot be held in hand and counted as in this study.

Interactions in the freshwater environment between hatchery and naturally produced salmonids are likely to disproportionately affect those species which spend the most rearing time in the river. Naturally produced steelhead, spring Chinook salmon, and coho salmon juveniles typically spend at least one year in freshwater (Healey 1991, Sandercock 1991, Moyle 2002). Fall Chinook salmon, however, are unambiguously ocean-type (Moyle 2002). Fall Chinook salmon juveniles emerge from the gravel in late winter or early spring, and within a matter of months, migrate downstream to the estuary and the ocean (Moyle 2002, Quinn 2005). Therefore, naturally produced steelhead, spring Chinook salmon, and coho salmon juveniles are more likely than fall Chinook salmon to experience competition for food and resources in the river, triggering mechanisms such as density dependent mortality (Kostow et al. 2003, Kostow and Zhou 2006), that may ultimately impact the populations of those species. It then follows that in the upper Trinity River, the stocks which have the lowest proportion of naturally

produced individuals returning to the upper Trinity River are coho salmon (~10%) and steelhead (~25%), while fall Chinook salmon have the highest proportion of naturally produced individuals (~40%) (Trinity River Flow Evaluation 1999, California Department of Fish and Game 2005). It should be noted that naturally produced salmonids have also been affected by reductions in available fry rearing habitat of the Trinity River in previous decades resulting from the erection of dams (Trinity River Flow Evaluation 1999, Record of Decision 2000).

Quantifying impacts on naturally produced salmon from predation by hatchery reared fish is one of the steps that can help inform decision makers. For example, one might estimate the number of fry that survive to reach smoltification as a result of a habitat improvement project that would not have survived to smoltification otherwise. This benefit to natural production as a result of a project like habitat enhancement could then be compared with the detriment to natural production caused by predation. This would let managers gauge, with a cost-benefit type analysis, the potential for conflict between the operational regime of a hatchery and river restoration projects. For instance, of 44 different river restoration sites aimed at improving the survival rate of naturally produced fry in the Trinity River, 4 are located in the study reach for this project. Benefits to natural production resulting from these habitat enhancement projects could be compared to the results of this study.

Northern-California Native American Tribes, the State of California, and the U.S. Government have agreed that restoring naturally produced salmonids to “pre-dam levels” is a priority, collectively creating and operating the Trinity Management Council, and the

Trinity River Restoration Program (Trinity River Flow Evaluation 1999, Record of Decision 2000). When ecological and genetic interactions between hatchery and natural salmonids are placed in the greater context of Trinity River restoration, the interactions between these fish has the potential to become problematic, as the goals of Trinity River Restoration Program may be in conflict with the current management regime of hatchery fish. Whether or not the extent of the conflict warrants action by river and hatchery managers is a decision that should be carefully considered.

Other river systems that might be at risk for predation by hatchery salmonids on naturally produced salmonids are those which have similar conditions as that on the Trinity River. Those conditions are relatively low flows, low turbidity, and release location near areas in which spawning adults congregate to build redds.

REFERENCES

Agresti, A., and B Coull. 1998. Approximate is better than 'exact' for interval estimation of binomial proportions. The American Statistician 52: 119-126.

Ando, D., T. Kitamura, and S. Mizuno. 2005. Quantitative analysis of body silvering during smoltification. North American Journal of Aquaculture 67:160–166.

Araki, H., B. Cooper, and M. S. Blouin. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science 318:100–103.

Beauchamp, D. A. 1990 Seasonal and diel food habits of rainbow trout stocked as juveniles in Lake Washington. Transactions of the American Fisheries Society 119: 475–482.

Beauchamp, D. A. 1995. Riverine predation on sockeye salmon fry migrating to Lake Washington. North American Journal of Fisheries Management 15:358-365.

Beauchamp, D. A., M. G. LaRiviere, and G. L. Thomas. 1999. Evaluation of competition and predation as limits to juvenile kokanee and sockeye salmon production in Lake Ozette, Washington. North American Journal of Fisheries Management 15:193-207.

Beeman, J. W., D. W. Rondorf, M. E. Tilson, and D. A. Venditti. 1995. A nonlethal measure of smolt status of juvenile steelhead based on body morphology. Transactions of the American Fisheries Society 124:764-769.

Berejikian, B. A., S. B. Mathews and T. P. Quinn. 1996. Effects of hatchery and wild ancestry and rearing environments on the development of agonistic behavior in steelhead trout (*Oncorhynchus mykiss*) fry. Canadian Journal of Fisheries and Aquatic Sciences 53: 2004-2014.

Bumgarner, J., M Schuck, S. Martin, J. Dedloff, and L. Ross. Lyons Ferry Complex Hatchery Evaluation: Summer steelhead and trout report 1998, 1999, and 2000 run years. United States Fish and Wildlife Service Lower Snake River Compensation Plan Office, Boise, Idaho. Cooperative Agreements 1411-98-J057, 14110-99-J070, 14110-0-J049. Washington Department of Fish and Wildlife report FPA02-09.

California Department of Fish and Game. 2002. Status review of California coho salmon north of San Francisco. Report to The California Fish and Game Commission. Candidate Species Status Review Report 2002-3, 336 pp.

California Department of Fish and Game. 2005. Trinity River Basin salmon and steelhead monitoring project 2003-2004 season. Northern California-North Coast Region. Redding, CA. 142 pp.

Cannamela, D.A. 1993. Hatchery steelhead smolt predation of wild and natural juvenile Chinook salmon fry in the upper-Salmon River, Idaho. Idaho Department of Fish and Game. Boise, Idaho.

Chrisp, E. Y. and T. C. Bjornn. 1978. Parr-smolt transformation and seaward migration of wild and hatchery steelhead trout in Idaho. Forest, Wildlife, and Range Experiment Station. Project F-49-12, Salmon and Steelhead Investigation. Final Report. Moscow, Idaho.

Cone, R. S. 1989. The need to reconsider the use of condition indices in fishery science. Transactions of the American Fisheries Sociely 118:510-514.

Crozier, W. W. 1998. Genetic implications of hatchery rearing in Atlantic Salmon: effects of rearing environment on genetic composition. Journal of Fish Biology 52: 1014-1025.

Einum, S. and I. A. Fleming. 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. Journal of Fish Biology 50: 634–651.

Elliott, J. M. 1991. Rates of gastric evacuation in piscivorous brown trout, *Salmo trutta*. Freshwater Biology 25: 297-305.

Fleming, I. A., K. Hindar, I. B. Mjölneröd, B. Jonsson, T. Balstad and A. Lamberg. 2000. Lifetime success and interactions of farm salmon invading a native population. Proceedings of the Royal Society of London B 267: 1517-1523.

Fleming, I. A., B. Jonsson, M. R. Gross, and A. Lamberg. 1996. An experimental study of the reproductive behavior and success of farmed and wild Atlantic Salmon (*Salmo salar*). Journal of Applied Ecology 33:893-905.

Fritts, A. L. and T. N. Pearsons. 2004. Smallmouth bass predation on hatchery and wild salmonids in the Yakima River, Washington. Transactions of the American Fisheries Society 133(4):880–895.

Good, T.P., R.S. Waples, and P. Adams (editors). 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. U.S. Department of Commerce, NOAA Techical Memorandum NMFS-NWFSC-66, 598 pp.

Gregory, R. S. and C. D. Levings. 1998. Turbidity reduces predation on migrating juvenile pacific salmon. Transactions of the American Fisheries Society 127: 275-285.

Grey, G. 1999. Covariances in multiplicative estimates. Transactions of the American Fisheries Society 128:475-482.

Haner, P. V., J. C. Faler, R. M. Schrock, D. W. Rondorf, and A. G. Maule. 1995. Skin reflectance as a nonlethal measurer of smoltification for juvenile salmonids. North American Journal of Fisheries Management 15:814-822.

Hard, J. J., B. A. Berejikian, E. P. Tezak, S. L. Schroder, C. M. Knudsen and L. T. Parker. 2000. Evidence for morphometric differentiation of wild and captively reared adult coho salmon: a geometric analysis. Environmental Biololgy of Fishes 58:61-73.

Hatchery Scientific Review Group. 2004. Hatchery reform: principles and recommendations of the hatchery scientific review group. Long Live the Kings, 1305 Fourth Avenue, Suite 810, Seattle, WA 98101. Available at: www.hatcheryreform.org. Contacted on March 2008.

Hawkins, S. W., and J. M. Tipping. 1999. Predation by juvenile hatchery salmonids on wild fall chinook salmon fry in the Lewis River, Washington. California Fish and Game 85:124-129

He, E. and W. A. Wurtsbaugh. 1993. An empirical model of gastric evacuation rates for fish and an analysis of digestion in piscivorous brown trout. Transactions of the American Fisheries Society 122: 717-730.

Healey, M.C. 1991. Life history of coho salmon (*Oncorhynchus tshawytscha*). Pages 313-393 in C. Groot and L. Margolis, editors Pacific salmon life histories. University of British Columbia Press, Vancouver, British Columbia, Canada.

Henderson, M. A., and A. J. Cass. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon (*Oncorhyncus nerka*). Canadian Journal of Fisheries and Aqautic Sciences. 48:988-994.

Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences. 47: 2181-2194

Jokikokko, E., I. Kallio-Nyberg, I. Saloniemi and E. Jutila. 2006. The survival of semi-wild, wild and hatchery-reared Atlantic salmon smolts of the Simojoki River in the Baltic Sea. Journal of Fish Biology 68: 430-442.

Jonasson B.C., R.W. Charmichael and T.A. Whitesel. 1994. Residual hatchery steelhead: Characteristics and potential interactions with spring Chinook salmon in northeast Oregon. Oregon Department of Fish and Wildlife. Salem, Oregon.

Jonasson B.C., R.W. Charmichael and T.A. Whitesel. 1995. Residual hatchery steelhead: Characteristics and potential interactions with spring Chinook salmon in northeast Oregon. Oregon Department of Fish and Wildlife. Salem, Oregon.

Jonnson, B. 1997. A review of ecological and behavioural interactions between cultured and wild Atlantic salmon. ICES Journal of Marine Science 54: 1031-1039.

Jonnson, N., B. Jonnson and L. P. Hansen. 2003. The marine survival and growth of wild and hatchery-reared Atlantic salmon. Journal of Applied Ecology 40: 900-911.

Kennedy, G. J. A. and C. D. Strange. 1986. The effects of intra- and inter-specific competition on the survival and growth of stocked juvenile Atlantic salmon, *Salmo salar* L., and resident trout, *Salmo trutta* L., in an upland stream. Journal of Fish Biology 28: 479–489

Kostow, K. E. 2004. Differences in juvenile phenotypes and survival between hatchery stocks and a natural population provide evidence for modified selection due to captive breeding. Canadian Journal of Fisheries and Aquatic Sciences 61: 577–589.

Kostow, K. E., A. R. Marshall and S. R. Phelps. 2003. Naturally spawning hatchery steelhead contribute to smolt production but experience low reproductive success. Transactions of the American Fisheries Society 132:780–790.

Kostow, K. E. and S. Zhou. 2006. The Effect of an introduced summer steelhead hatchery stock on the productivity of a wild winter steelhead population. Transactions of the American Fisheries Society 135: 825-841.

Levin, P. S., R. W. Zabel and J. G. Williams. 2001. The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. Proceedings of the Royal Society of London B 268: 1153–1158.

Light, R.W., P.H. Alder, and D.E. Arnold. 1983. Evaluation of gastric lavage for stomach analyses. North American Journal of Fisheries Management 3:81-85.

Lynch, M. and M. O'Hely. 2001. Captive breeding and the genetic fitness of natural populations. Conservation Genetics 2: 363–378.

Martin, S. W., A. E. Viola, and M.L. Schuck. 1993. Investigations of the interactions among hatchery reared summer steelhead, rainbow trout, and wild spring Chinook salmon in southeast Washington. Washington Department of Fish and Wildlife. Olympia, Washington. Report # 93-4.

Mather, M.E. 1998. The role of context-specific predation in understanding patterns exhibited by anadromous salmon. Canadian Journal of Fisheries and Aquatic Sciences 55 (Suppl. 1): 232-246.

McConnaughey, J. 1999. Predation by coho salmon smolts (*Oncorhynchus kisutch*) in the Yakima and Klickitat Rivers. Report by the Yakima Indian Nation Fisheries Program, Yakima, Washington.

McGinnity, P., P.Prodo, A. Ferguson, R. Hynes, N. O´ Maoile´idigh, N. Baker, D. Cotter, B. O'Hea1, D. Cooke, G. Rogan, J. Taggart and T. Cross. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proceedings of the Royal Society of London B 270: 2443–2450.

McLean, J. E., P. Bentzen and T. P. Quinn. 2003. Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead trout, (*Oncorhynchus mykiss*) through the adult stage. Canadian Journal of Fisheries and Aquatic Sciences 66: 443-440.

McMichael, G.A. and T.N. Pearsons. 2001. Upstream movement of residual hatchery steelhead into areas containing bull trout and cutthroat trout. North American Journal of Fisheries Management 21: 943-946.

McMichael, G.A., T.N. Pearsons, and S.A. Leider. 1999. Behavioral interactions among hatchery-reared steelhead smolts and wild *Oncorhyncus mykiss* in natural streams. North American Journal of Fisheries Management 19: 948-956.

McMichael, G.A., C. S. Sharpe and T.N. Pearsons. 1997. Effects of residual hatchery-reared steelhead on growth of wild rainbow trout and spring chinook salmon. Transactions of the American Fisheries Society 126: 230–239.

Mesa, M. G. 1991. Variation in feeding, aggression, and position choice between hatchery and wild cutthroat trout in an artificial stream. Transactions of the American Fisheries Society 120: 723 727.

Miyakoshi, Y., M. Nagata, and S. Kitada. 2001. Effect of smolt size on post release survival of hatchery-reared masou salmon *Oncorhynchus masou*. Fisheries Science 67:134-137

Moyle, P. B. 2002. Inland fishes of California. University of California Press. Berkeley, California.

Naughton, G. P. D. H. Bennett, and K. B. Newman. 2004. Predation on juvenile salmonids by smallmouth bass in the Lower Granite Reservoir System, Snake River. North American Journal of Fisheries Management 24: 534–544.

Newman, R. L. 2002. Steelhead volitional release experiment Squaw Creek Pond, Idaho. Report to United States Fish and Wildlife Service, Lower Snake River Compensation Plan Office, Boise Idaho. Agreement 14110-9J007. Idaho Fish and Game Report Number 02-49.

National Weather Service. 2008. Local climate records. National Weather Service, Eureka, California. Available at www.wrh.noaa.gov/eka/climate. Contacted on March 2008.

Partridge, F. E. 1985. Effect of steelhead smolt size on residualism and adult return rates. Report by Idaho Department of Fish and Game to the U.S. Department of the Interior, Lower Snake River Fish and Wildlife Compensation Plan. Contract 14-16-001-83605 (1983 segment).

Partridge, F. E. 1986. Effect of steelhead smolt size on residualism and adult return rates. Report by Idaho Department of Fish and Game to the U.S. Department of the Interior, Lower Snake River Fish and Wildlife Compensation Plan. Contract 14-16-001-83605 (1984 segment).

Pearse, P.E., C. J. Donohoe, and J. C. Garza. 2007. Population genetics of steelhead (*Oncorhynchus mykiss*) in the Klamath River. Environonmental Biololgy of Fish 80:377–387.

Pearsons, T. N. and A. L. Fritts. 1999. Maximum size of Chinook salmon consumed by juvenile coho salmon. North American Journal of Fisheries Management 19:165–170.

Pollard, H. A. II and T. C. Bjornn. 1973. The effects of angling and hatchery trout on the abundance of juvenile steelhead trout. Transactions of the American Fisheries Society 102: 745–752.

Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, WA.

Record of Decision. 2000. U.S. Department of the Interior Record of Decision Trinity River Mainstem Fishery Restoration Final Environmental Impact Statement/Environmental Impact Report. Available at www.trrp.net/documents/ROD.pdf. Accessed January 2008.

Reisenbichler, R. R. and J. D. McIntyre. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. Journal of Fisheries Research Board of Canada 34: 123-128.

Reisenbichler, R. R. and S. P. Rubin. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. ICES Journal of Marine Science 56: 459-466.

Rhine, T. D., J. L. Anderson, and R. S. Osborne. 2002. Sawtooth fish hatchery volitional release experiment: A stocking method to reduce residual steelhead in the upper Salmon River, Idaho. Report to the U.S. Fish and Wildlife Service, Lower Snake River Compensation Plan Office, Boise, Idaho. Idaho Fish and Game Report Number 02-55.

Robertis, A. D., C. H. Ryer, A. Veloza, and R. D. Brodeur. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Canadian Journal of Fisheries and Aquatic Sciences 60:1517-1526.

Ruggerone, G. T. (1989) Gastric evacuation rates and daily ration of piscivorous coho salmon, Oncorhynchus kisutch Walbaum. Journal of Fish Biology 34, 451–463.

Ruggerone, G. T. and D. E. Rogers. 1992. Predation on sockeye salmon fry by juvenile coho salmon in the Chignik Lakes, Alaska: Implications for salmon management. North American Journal of Fisheries Management 12: 87-102.

Saisa, M., M. Koljonen and Jaana Tahtinen. 2003. Genetic changes in Atlantic salmon stocks since historical times and the effective population size of a long-term captive breeding programme. Conservation Genetics 4: 613-627.

Saloniemia, I., E. Jokikokko, I. Kallio-Nybergc, E. Jutilad and P. Pasanene. 2004. Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. ICES Journal of Marine Science 61:782-787

Sandercock, F.K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). Pages 397-445 in C. Groot and L. Margolis, editors Pacific Salmon Life Histories. University of British Columbia Press, Vancouver, British Columbia, Canada.

Schmidt, S. P. and E. W. House. 1979. Precocious sexual development in hatchery-reared and laboratory maintained male steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada. 36:90-93.

Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. 2nd edition. Griffin, London. Chapters 3-5.

Seelbach, P. W. 1987. Smolting success of hatchery-raised steelhead planted in a Michigan tributary of Lake Michigan. North American Journal of Fisheries Management 7:223-231.

Thompson, S. K. 2002. Sampling. Wiley Series in Probability and Statistics, New York, NY.

Tipping, J. M., R. V. Cooper, J. B. Byrne, and T. H. Johnson. 1995. Length and condition factor of migrating and nonmigrating hatchery-reared winter steelhead smolts. The Progressive Fish-Culturist 57:120-123.

Tipping, J. M. 1997. Effect of smolt length at release on adult returns of hatchery-reared winter steelhead. The Progressive Fish-Culturist 59:310-311.

Trinity River Flow Evaluation 1999. Report by the U.S. Fish and Wildlife Service and Hoopa Valley Tribe to the Secretary, U.S. Department of Interior, Washington, D.C. Available at http://www.fws.gov/arcata/fisheries/reportsDisplay.html. Contacted on November 2007.

United States Fish and Wildlife Service. 2007. Trinity River redd survey update. Progress Report. United States Fish and Wildlife Service. Arcata Fish and Wildlife Office, Arcata, California.

United States Naval Observatory. 2007. United States Naval Observatory sun or moon rise/set table for one year. Available at http://aa.usno.navy.mil/data/docs/RS_OneYear.php. Contaced on November 2007.

Viola, A.E. and Schuck, M.L. 1995. A method to reduce the abundance of residual hatchery steelhead in rivers. North American Journal of Fisheries Management 15: 488-493.

Ward, B.R. and P.A. Slaney. 1988. Life history and smolt-to-adult survival of Keogh River steelhead Trout (*Salmo gairdneri*) and the relationship to smolt size. Canadian Journal of Fisheries and Aquatic Sciences 45: 1110-1122

Wessel, M. L., W. W. Smoker and J. E. Joyce. 2006. Variation of morphology among juvenile Chinook salmon of hatchery, hybrid, and wild origin. Transaction of the American Fisheries Society 135: 333-340.

Whitesel, T.A., B.C. Jonasson and R.W. Charmichael. 1993. Residual hatchery steelhead: Characteristics and potential interactions with spring Chinook salmon in northeast Oregon. Oregon Department of Fish and Wildlife. Salem, Oregon.

Yurok Tribal Fisheries Program. 2008. Predation by hatchery steelhead on natural salmonid fry in the upper-Trinity River, California, 2005. Yurok Tribal Fisheries Program, Weitchpec, CA.

Zydlewski G. B., G. H., T. Dubreuil, B. Letcher, S. Casey, and J. Zydlewski. 2006. Remote monitoring of fish in small streams. Fisheries 31:492–502.