POSSIBLE DECLINE IN THE HALF-POUNDER LIFE HISTORY AMONG TRINITY RIVER STEELHEAD (*Oncorhynchus mykiss*)

by

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ABSTRACT

Possible Decline of the Half-Pounder Life History among Trinity River Steelhead
(*Oncorhynchus mykiss*)

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Steelhead, *Oncorhynchus mykiss*, exhibit a wide variety of life histories, including a unique "half-pounder" life history, primarily found in Northern California and Southern Oregon. A half-pounder is an immature steelhead that returns to freshwater within about four months of ocean entry. I estimated the frequency of the half-pounder life history among wild and hatchery adult steelhead from the Trinity River using scale analysis. Hatchery smolts currently are released as age-1 smolts from Trinity River Hatchery and are substantially larger than their wild counterparts. Wild smolt ages range from 1 through 3, with most smolts ages 1 or 2. To determine whether age- or size-at-ocean entry affects the tendency for an individual steelhead to exhibit half-pounder life history, I examined over 2,000 scale samples from wild and hatchery adult steelhead collected intermittently over a 27-year period from 1982 through 2009. Age at ocean entry of wild steelhead smolts appeared to be strongly associated with the proportion of adult steelhead returning that have undergone a half-pounder run. Wild smolts entering the ocean as age-1 smolts were more likely to undergo a half-pounder migration than age-2 or age-3 smolts. Based on logistic regression analyses, the size at the end of freshwater zone (prior to estuary or ocean entry) was inversely correlated with half-pounder proportions among returning wild adults. Thus, wild age-2 smolts that were smaller at the end of the freshwater zone were more likely than larger steelhead smolts of the same age to undergo the half-pounder migration. The tendency of hatchery smolts to mature as half-pounders

was generally quite low (10-20%), especially in recent years, and appears related to the large size at which steelhead have been released from Trinity River Hatchery since the mid-1990s.

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INTRODUCTION

Steelhead, *Oncorhynchus mykiss*, are native to the west coast of North America and range from Southern California to Alaska. The species is also present in the western North Pacific Ocean. They typically spend between one and three years in freshwater before migrating to the ocean and may return to freshwater after one to two winters in the ocean (Kesner and Barnhart 1972, Busby et al. 1996). Steelhead are iteroparous and may spawn up to four times in exceptional cases (Busby et al. 1996). Distinct reproductive ecotypes - summer-run (stream-maturing), fall-run (ocean-maturing) and winter-run (ocean-maturing) - return to freshwater in different time periods, but all ecotypes typically spawn during winter and spring months (Busby et al. 1996).

Peak migration of fall-run adult steelhead into California's Trinity River typically occurs in the months of October or November (Sinnen et al. 2009). Most spawning of wild adult steelhead in the Trinity River basin tributaries occurs between the months of February and April (LaFaunce 1964, Rogers 1971, Garrison 2000, 2002). Juvenile steelhead typically rear in tributary or mainstem habitats from one to three years before migrating to the ocean, with the majority of smolts spending either one or two years in freshwater (United States Fish and Wildlife Service 1998, Hopelain 1998). Peak outmigration of Trinity River Hatchery steelhead smolts past the downstream migrant trap at river kilometer 34 (rkm, measured from confluence with Klamath River) typically occurs between mid-March through June (United States Fish and Wildlife Service 1998, Pinnix et al. 2007). Peak outmigration of Trinity River wild steelhead smolts typically occurs slightly later in the spring and in some years can last until July (Pinnix and Quinn 2009). Catches of wild steelhead smolts in the Klamath River estuary typically peak in the months of May or June, but steelhead smolts are also captured during the entire summer (Wallace 2003). Hatchery origin steelhead only made up a small portion (10-15%) of all steelhead smolts captured during surveys in the estuary, with highest catches occurring during the early portion of the summer suggesting that hatchery steelhead may exit the estuary earlier than wild steelhead (Wallace 2003).

An unusual freshwater return of steelhead as immature fish following 3-5 months of initial ocean feeding and growth has been noted in a small number of river systems. Such fish are termed “half-pounders”. Studies of the half-pounder life history among summer and fall runs of steelhead have focused on the Eel and Klamath rivers in Northern California (Snyder 1925, Kesner and Barnhart 1972, Hopelain 1998) and on the Rogue River in Southern Oregon (Everest 1973, Satterwaithe 1988). Similar life histories have been reported in Kamchatka among native *O. mykiss* (Savvaitova et al. 2005) and among introduced *O. mykiss* in Patagonia (Pascual et al. 2001). However, the half-pounder life history has not been reported in other rivers throughout the range of steelhead. In the Klamath and Rogue rivers, half-pounders are smaller in size than adult steelhead and only a small fraction are sexually mature. After migration into freshwater (August – October) half-pounders typically migrate relatively short distances upstream compared with mature adult steelhead (Kesner and Barnhart 1972, Everest 1973) and, in contrast to adult steelhead, actively feed during their residence in freshwater (Kesner and Barnhart 1972). Half-pounders migrate back to the ocean during February through April of the succeeding year (Satterwaithe 1988, United States Fish and Wildlife Service 1991, 1994).

Everest (1973) and Hopelain (1998) used scale analysis (presence or absence of a half-pounder check) to estimate the prevalence of the half-pounder life history among returning adult steelhead in the Rogue and Klamath rivers, respectively. In the Rogue River, Everest (1973) found that 97% of returning summer/fall run steelhead exhibited the half-pounder life history. Hopelain (1998) found similar results from the Shasta, Scott, and Salmon Rivers and from Bogus Creek and Iron Gate Hatchery in the Klamath River based on data collected from 1980-1982. Over the same period of data collection, however, Hopelain (1998) found that only 32.0% and 35.3% of adult steelhead exhibited the half-pounder life history in the North Fork Trinity River and South Fork Trinity River, respectively. In contrast, among adult steelhead captured during fall 1982 at the Willow Creek weir on the mainstem Trinity River, 80.0% had first returned as half-pounders (Hopelain 1998).

The size and(or) age at which a salmonid undergoes smoltification has been shown to increase adult returns among adults in a variety of species including wild and hatchery steelhead (Ward and Slaney 1988, Tipping 1997), hatchery sea-run cutthroat (*O. clarki*) (Tipping 1986), coho salmon (*O. kisutch*) (Holtby et al. 1990), wild and hatchery Atlantic salmon (*Salmo salar*) (Saloniemi et al. 2004), white-spotted charr (*Salvelinus leucomaenis*) (Yamamoto et al. 1999), and Chinook salmon (*O. tshawytscha*) (Martin and Wertheimer 1989). Bond et al. (2008) showed that wild and hatchery steelhead smolts that entered the ocean at smaller sizes experienced very low ocean survival compared to wild steelhead smolts that entered at larger sizes. Similar results were found by Melnychuk et al. (2007) using acoustic tags implanted in out-migrating steelhead smolts in British Columbia. Early marine growth, estimated from scale radii, has also been shown to influence survival during later stages of life for hatchery pink salmon (*O. gorbuscha*) (Moss et al. 2005, Cross et al. 2009) in the Gulf of Alaska and for coho salmon (Holtby et al. 1990, Beamish et al. 2004) in British Columbia.

Length-at-age may not, however, be the only factor affecting early marine survival and growth of salmonids. Zabel and Achord (2004) showed that size of juvenile Chinook salmon alone does not confer survival to next life stage. Other factors such as ocean conditions, timing of ocean entry, and interactions among these factors may affect the marine survival of salmonids (Hansen and Quinn 1998, Ryding and Skalski 1999, Welch et al. 2000).

For half-pounder steelhead to return to freshwater after only a few months in the ocean, they must not travel extreme distances in the ocean, but must instead stay in nearshore waters. Indeed, Pearcy et al. (1990) suggested that California steelhead populations may reside in the strong upwelling zone off northern California and southern Oregon. Straying of hatchery half-pounders from Klamath River hatcheries to the Rogue River has been documented during beach seining in the lower Rogue River estuary, suggesting that half-pounders may not make extensive ocean migrations (Everest 1973, Satterthwaithe 1988) and that homing to the natal stream may be of less importance for half-pounders than for adults which exhibit lower straying rates (Satterthwaithe 1988).

Everest (1973) and Hopelain (1998) conducted the most thorough studies on the half-pounder life history in the Rogue and Klamath rivers, respectively. While there has been subsequent sporadic monitoring of the prevalence of the half-pounder life history among returning adult steelhead in the Rogue River (Satterwaithe 2002), no studies have compared temporal trends in life histories between wild and hatchery steelhead. No studies to date have examined what biological factors may influence an individual steelhead's tendency to exhibit the half-pounder life history or have examined the interannual variation in the prevalence of the half-pounder life history.

The purposes of my study were to: 1) use scale pattern analysis to estimate the frequency of the half-pounder life history in wild and hatchery stocks from archived scales and from contemporary collections (1982 - 2009) from the Trinity River; and, 2) identify potential biological factors that may affect an individual steelhead's tendency to exhibit the half-pounder life history.

Study Site

The Trinity River is the largest tributary of the Klamath River, draining approximately 7,600 square kilometers in northern California (Figure 1). The headwaters originate in the Trinity Alps Yolla Bolly Mountains (South Fork). Lewiston Dam at river km 182.5 blocks upstream migration of anadromous fishes including spring- and fall-run Chinook salmon, coho salmon, summer-, fall-, and winter-run steelhead and Pacific lamprey (*Entosphenus tridentatus*). Trinity River Hatchery is located at the base of Lewiston Dam and is operated by the California Department of Fish and Game and the Hoopa Valley Tribe to mitigate for losses of upstream spawning habitats due to the construction of Trinity Dam in 1963. Between 1979 and 2007, releases of steelhead smolts from Trinity River Hatchery averaged 633,493 per year (Trinity River Hatchery Annual Reports, 1980 – 2007).

Since 1998, all Trinity River Hatchery steelhead have received an adipose fin clip to identify hatchery origin, and released as age-1 smolts, typically in mid to late March. Prior to 1998, a variety of fin clip types were used to identify brood year and age at

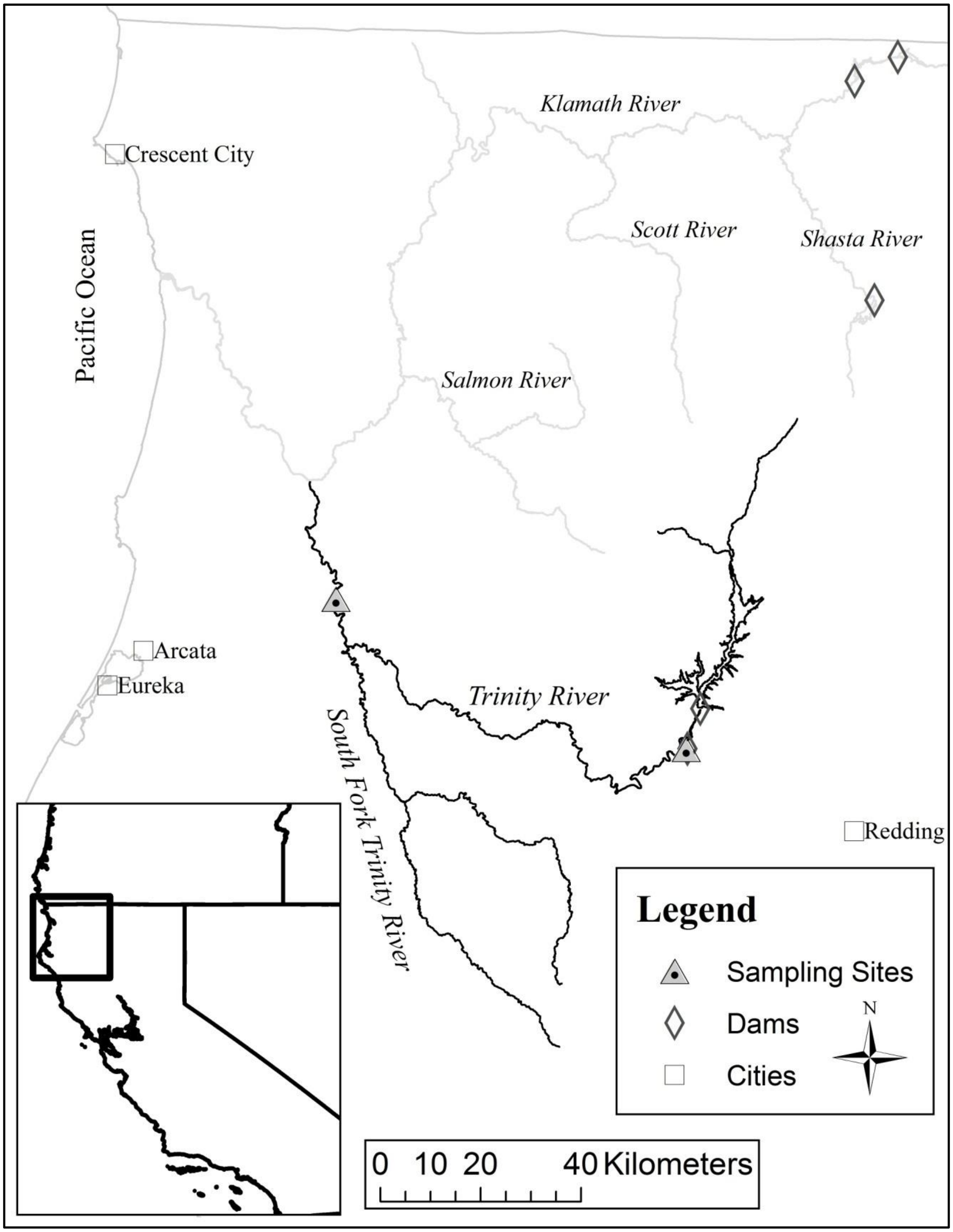

Figure 1. Locations of Willow Creek weir near Willow Creek, California (rkm 36.5), Lewiston Dam (site of Trinity River Hatchery), rkm 182.5.

release. All or a portion of the releases were released unclipped during the release years: 1982-1989, 1996 and 1997. Only unmarked hatchery half-pounders were present during run years 1982 and 1996 and unmarked hatchery adults were present as repeat spawners (2^{nd} and(or) 3^{rd} time repeat spawners) in 1991 and(or) 1992 respectively. Therefore, no unmarked hatchery adult steelhead were included in estimates of half-pounder proportions (see Estimation of Half-Pounder Proportions).

The Willow Creek weir has been operated since 1979 at several locations near Willow Creek, California, and from 2007 to 2009. It was installed at rkm 36.5 (40º 58' 29.85" N, 123º 38' 8.61" W) (Sinnen et al. 2009). The Willow Creek weir traps Chinook and coho salmon and adult steelhead, but very few half-pounders. Due to the spacing of pickets on the weir, the few half-pounders that were collected were only the largest half-pounders. Therrefore, the weir collected half-pounders that were much larger than average half-pounders in run (Sinnen et al. 2009). The weir typically is operated four to five days per week from mid-August to late-November or early-December, depending on river flows.

METHODS

Complexity of Steelhead Life History and Assessment of Tendency to Mature as Half-Pounders

One of the primary objectives of this research was to document temporal variability and a speculated decreasing trend of Trinity River steelhead to return as half-pounders. Steelhead life history can be extremely variable and the complexity of the life history schedule makes it difficult to develop an unbiased estimate or index of the tendency to return as a half-pounder. In the Trinity River, age of wild smolts ranges from one to three years, steelhead may or may not return as half-pounders, adults may spend one or two years in the ocean prior to their maiden spawning run, and some adults may spawn multiple times. Therefore, estimation of the proportion of adult steelhead that have undergone a half-pounder run is complicated by two, and possibly, three, different factors; 1) the proportion of steelhead that actually go on a half-pounder run, 2) relative survival of steelhead undergoing the half-pounder migration as compared to steelhead remaining in the ocean, and 3) number of years at sea (two or three summers) prior to return as an adult. These three factors no doubt vary interannually.

I developed a life history pathway model specific to steelhead in the Trinity River in order to: a) illustrate the complexity of the steelhead life history in the Trinity River, b) link life history of steelhead to life history notation developed by Hopelain (1998), c) investigate potential life history tradeoffs, and, d) identify expected proportion of steelhead exhibiting particular life histories. This model provides substantial insight into the complications of assessing the proportion of steelhead that have undergone a half-pounder migration (Appendix A).

Hopelain's (1998) general steelhead life history notation is:

a/h.ks or *a*/j.ks,

where: *a* = number of juvenile freshwater years to the left of the slash; "h" indicates that a half-pounder run occurred; j = number of saltwater years to the right of the slash; and, ks = the number of spawning runs (s). For example, 2/h.1s, denotes a steelhead that spent two years in freshwater prior to smolting, returned to freshwater as a half-pounder after one summer in the ocean and then returned as a mature adult on its first spawning run in its second ocean year. As another example, 1/1.2s, denotes a steelhead that spent only one year in freshwater prior to smolting, did not undergo a half-pounder run, made an initial spawning run after one year in the ocean, and survived to make a second spawning run. The following list describes the events of the most common life histories observed from Trinity River steelhead and the associated life history notation.

a/h = age *a* smolt; returning as a half-pounder

a/h.1s = age *a* smolt; returned as half-pounder and then again on first possible adult spawning run

a/1.1s = age *a* smolt; did not return as half-pounder, spent approximately 1.5 years in ocean and returned on first possible adult spawning run

a/h.2s = age *a* smolt; returned as half-pounder; returned on two successive spawning runs

a/1.2s = age *a* smolt; spent approximately 1.5 years in ocean and returned on two successive spawning runs

a/h.1.1s = age *a* smolt; returned as half-pounder; then spent approximately 1.5 years in ocean before returning on first adult spawning run *a*/2.1s = age *a* smolt; spent approximately 2.5 years in ocean before returning on first adult spawning run

Adult ages of returning steelhead were calculated by summing the number of years spent freshwater (smolt ages can be a = 1,2,3) and number of years spent in saltwater. Using the same example from above: a steelhead that exhibited the life history pattern, 2/h.1s, would have an adult age of 3+, since it spent two years in freshwater prior to smolting, returned to freshwater as a half-pounder after one summer in the ocean and then returned as a mature adult on its first spawning run in its second ocean year. The "+" is used since the 4^{th} annulus is not yet complete. As another example, 1/1.1s, would have an adult age of 2+, since it spent one year in freshwater prior to smolting, did not undergo a half-pounder run and made an initial spawning run after one year in the ocean.

The method used to assess the tendency of steelhead to return as half-pounders was to examine the scales of steelhead on their first possible adult spawning run and determine the fraction ($\hat{\rho}$) of steelhead that exhibited the half-pounder check (see Scale Preparation and Analysis). That is,

$$\hat{\rho} = \frac{n_a/h.1s}{(n_a/h.1s) + (n_a/1.1s)} \tag{1}$$

where $n_a/h.1s$ = observed number of first spawning adults that returned earlier as half-pounders, and $(n_a/h.1s) + (n_a/1.1s)$ = observed total number of first spawning adults. The expected value of $\hat{\rho}$, however, is not in general equal to $\sigma_{a|h}$, the probability of maturing as a half-pounder given smolt age a (see Appendix A).

Scale Preparation and Analysis

The most representative scales (those with little or no regeneration of scale focus and most consistent scale patterns) from individual steelhead (all sample years) were cleaned by soaking in water and rubbing gently on Rite-in-the-Rain® paper to remove mucus and other debris. Four to six scales, on average, were mounted between glass slides, which were then taped together. Moderately regenerated scales, (i.e., lacking most of the freshwater growth period) were typically not mounted, unless very few scales were collected for a particular fish. The most representative scale(s) were then photographed using a microscope-mounted digital camera (Retiga 2000R, 1600 x 1200 pixels; Qimaging, Surrey, British Columbia, Canada) and saved in tag image file format (TIFF). If a majority of scales collected from a single fish did not show similar life history events (i.e., same number of annuli or consistent saltwater features), then that fish was excluded from further analysis.

Image Pro Plus Professional software (version 6.2; Media Cybernetics, Silver Spring, Maryland) was used to measure various scale features. Measurements on circuli and annuli were taken to the nearest 0.001 mm on a line 15 degrees on either side of the longitudinal axis of the scale (Figure 2). Distances between circuli and identified life history events were recorded electronically. The locations of annuli and(or) checks were measured at the outer margin of annuli or checks. Conversions of measurements from digitized images to true scale measurements were made using the following calibration values: 184.000 pixels/mm (2X objective) and 369.049 pixels/mm (4X objective).

Life history events recorded on scales were identified and consisted of the following events: 1) freshwater annuli, 2) apparent end of the freshwater zone, 3) apparent point of ocean entrance, 4) half-pounder check or ocean annuli, and, 5) spawning checks. Freshwater annuli were identified by the most tightly spaced circuli

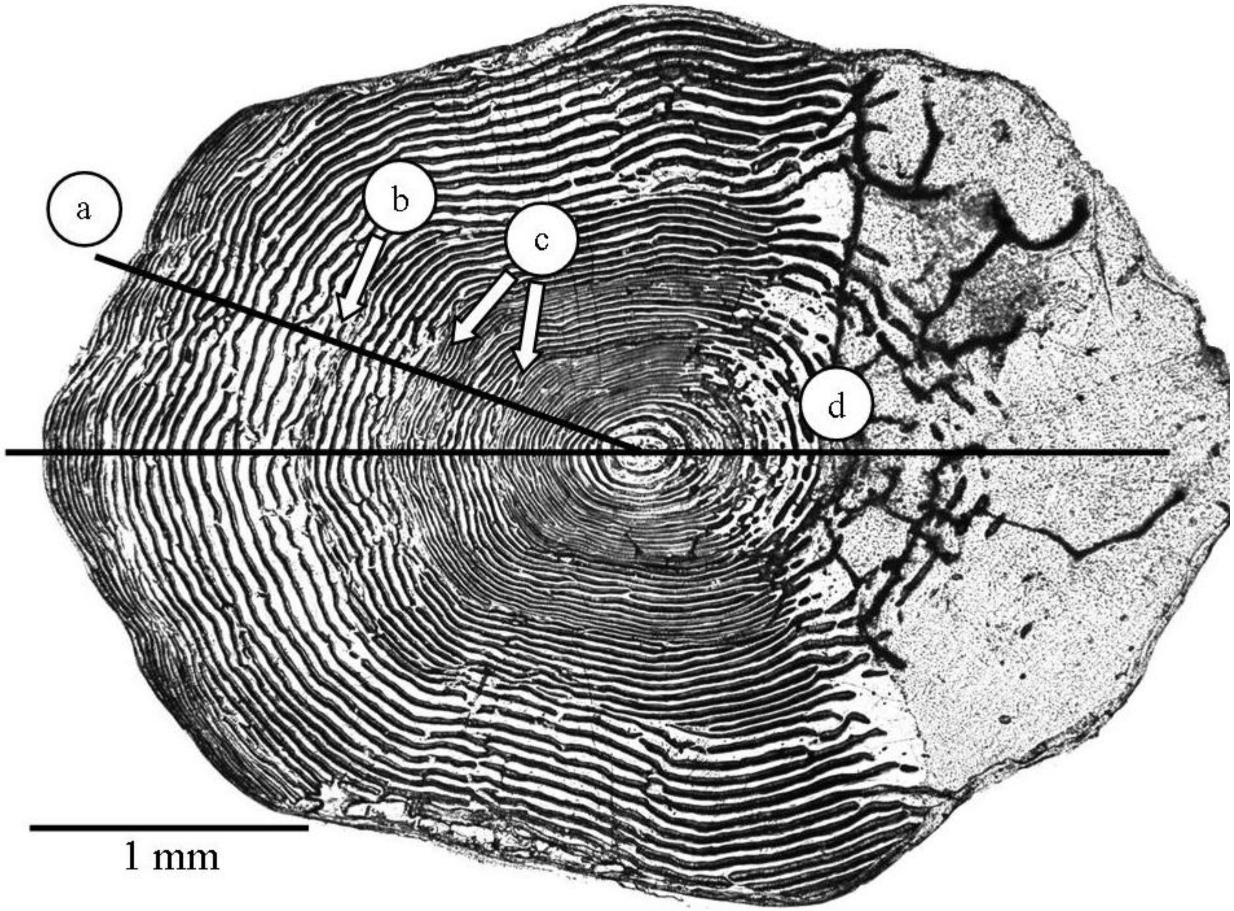

Figure 2. Image of scale from half-pounder steelhead collected from the Trinity River, California on 3 December 2008. Life history type 2/h (total age = 2+, nearly 3 years old, 353 mm fork length) showing the formation of half-pounder check on margin of scale. (a) 15^{o} offset; (b) apparent point of ocean entry; (c) two freshwater annuli, with 2nd annulus also at the end of the freshwater zone; and, (d) longitudinal scale axis. Region near the scale margin shows checking and decreased inter-circuli spacing typical of half-pounders during their freshwater residence.

and by convergence or "cutting off" of circuli. The apparent end of the freshwater zone was identified as the point where inter-circuli spacing ceased to be tightly spaced. Apparent ocean entry was identified by a significant increase of inter-circuli spacing as compared to the relatively tight spacing of freshwater growth or the intermediate spacing of apparent estuarine growth. Half-pounder and spawning checks were characterized by variable resorption of the scale and cutting over of circuli. Half-pounder checks generally fell between the back-calculated lengths of 250 mm and 410 mm (see Back-Calculation of Fork Lengths). For purposes of this study, regardless of size or maturity, a half-pounder was defined as a steelhead that spent one summer in the ocean and subsequently returned to freshwater to overwinter. An ocean or winter annulus was characterized by narrowing of circuli, but little or no resorption or cutting over of circuli when compared with a typical half-pounder check (Figure 3).

Quantitative Differentiation of Half-Pounder Checks versus Ocean Annuli

Because the visual classifications of half-pounder checks and ocean annuli were subjective and of uncertain reliability, I examined the comparative performance of subjective visual classifications with classifications based instead on quantitative scale measurements taken from about one-third of all adult samples (n = 607). I used scales collected from known half-pounders (n = 240) during their freshwater residence to develop a variety of measurements to objectively classify half-pounder checks and ocean annuli. Table 1 summarizes the developed quantitative measurements that were motivated by apparent visual differences of scale patterns for various life history types. Some of these measurements, or a combination of two or more, were thought to quantitatively differentiate steelhead that exhibited the half-pounder life

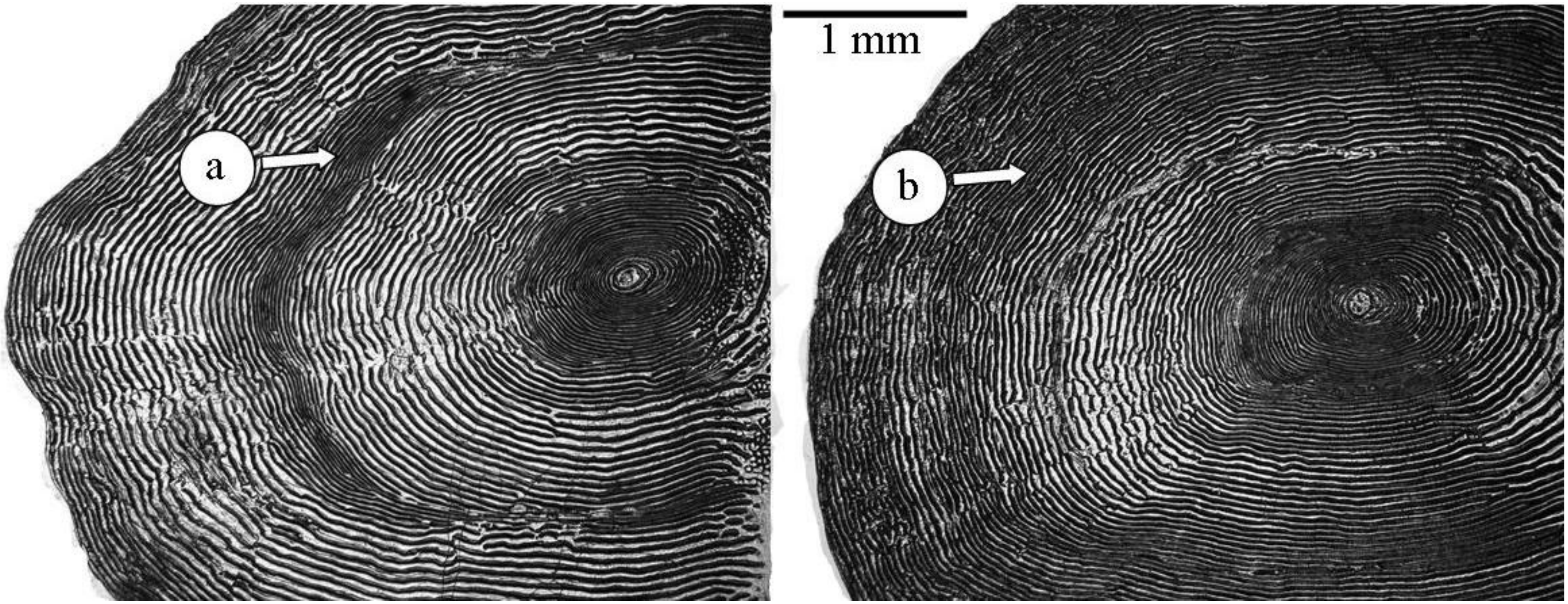

Figure 3. Images of scales from two age-3 steelhead from Trinity River, California. Left: Adult steelhead (550 mm FL) with life history type 2/h.1s (total age = 3+) showing half-pounder check. (a) denotes region of freshwater growth during half-pounder run during winter 2008/2009; Right: Adult steelhead (590 mm FL) with life history type 2/1.1s (total age = 3+): (b) denotes location of an ocean annulus during winter in ocean 2008/2009.

Table 1. Summary of 10 measurements taken on scales to differentiate between half-pounder checks and ocean annuli. All distances are in millimeters.

Measurement Number	Definition
1	Total width of the first five circuli inside suspected check
2	Total width of the first five circuli outside suspected check
3	Mean width of the first five circuli inside suspected check
4	Mean width of the first five circuli outside suspected check
5	Coefficient of variation of ten measurements inside and outside of suspected check
6	Circuli count from apparent ocean entry to end of suspected check
7	Circuli count from apparent end of freshwater zone to end of suspected check
8	Ratio of measurement 1/measurement 2
9	Ratio of measurement 3/measurement 4
10	Presence or absence of checking along scale margin near suspected check (likely indicating freshwater residence)

history and those that did not. The three most useful measurements were hypothesized to be the mean spacing and total width of the first five circuli posterior to a suspected check, because the width of five circuli of a half-pounder check should be less than the width on a scale showing an ocean annulus. Second, the coefficient of variation (CV) of ten circuli measurements posterior and anterior to the suspected check since the CV of a half-pounder check should be greater (tight circuli spacing during freshwater followed by wider spacing during subsequent ocean growth) (Figure 4) than the CV of an ocean annulus (more consistent spacing during ocean winter). Third, the ratios between the total width and mean circuli spacing posterior to and anterior to a suspected check: the ratio for an ocean annulus should be approximately equal to one whereas the ratio for a half-pounder check should be less than one. Coefficient of variation is calculated as:

$$CV = \frac{\sigma}{\mu}, \tag{2}$$

where, $\sigma =$ standard deviation of scale measurements and $\mu =$ mean of scale measurements. An additional measurement of potential value was hypothesized to be the presence or absence of checking or several scale erosion along the lateral margin of the scale, which from observations of known half-pounders during their freshwater residence, was substantial in some cases (see Figures 2 and 3(a)).

Stepwise logistic regression was used to identify the top three models for quantitative classification of half-pounder check or ocean annulus based on scale measurements identified in Table 1. Akaike Information Criterion (AIC) values, AIC weights, and goodness of fit were used to determine the most parsimonious model among the collection of candidate models (Stauffer, 2008). Goodness-of-fit of the top three candidate models was evaluated by using a leave-one-out algorithm which calculates new

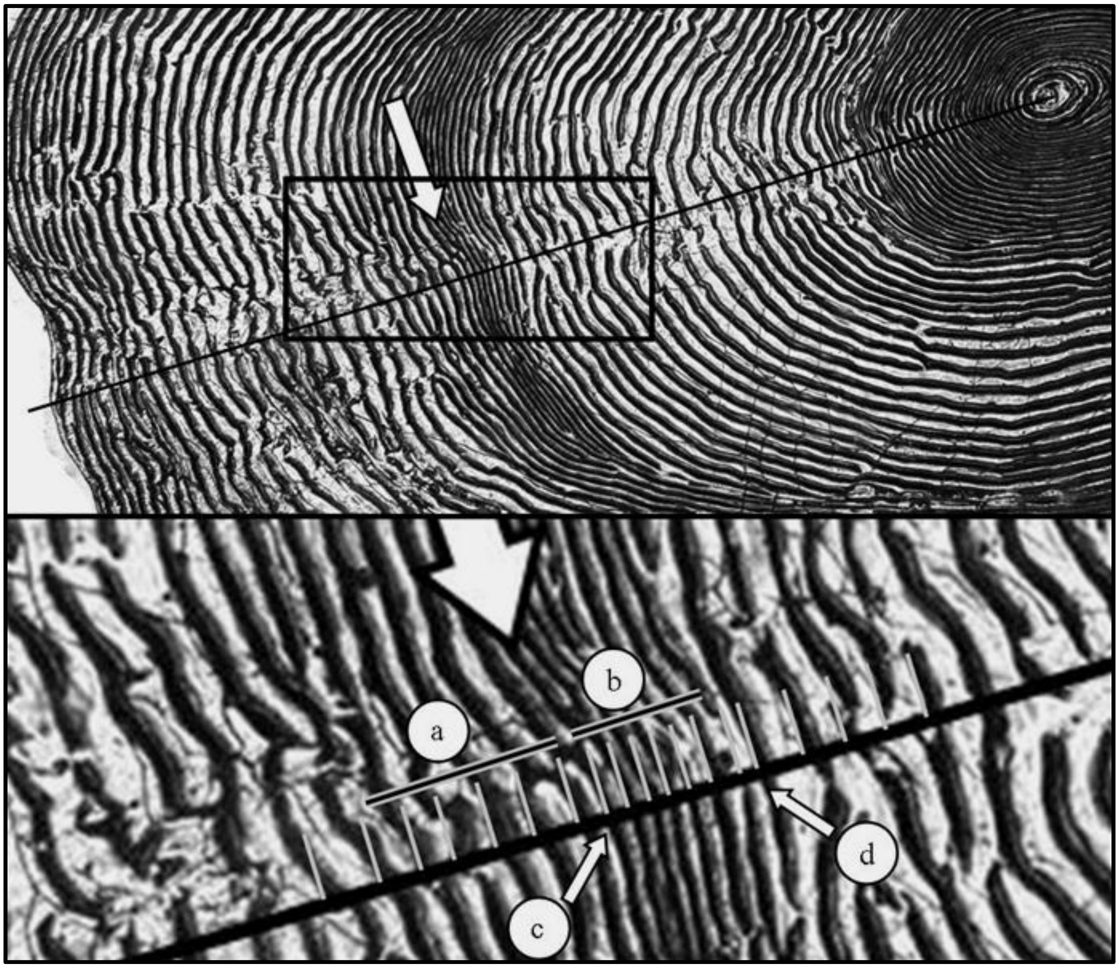

Figure 4. Image of scale from adult steelhead (550 mm FL) from Trinity River, California. Top: Scale from adult steelhead, life history type 2/h.1s (total age = 3+) showing half-pounder check (550 mm); bottom: magnified section showing measurements (a & b) and locations of beginning (d) and end of freshwater residence (c). Measurement (a) is the scale width in millimeters from end of the half-pounder check to five circuli anterior to the half-pounder check and (b) is scale width from end of half-pounder check to five circuli posterior to the half-pounder check. Note the difference in relative spacing of circuli between the measurements (a) and (b).

predicted probabilities without one observation, then compares that observation (0 or 1) with the predicted outcome (0 or 1). Predicted probabilities from each model were converted to predicted outcomes, either a half-pounder check or ocean annulus, and each model prediction was then compared to the observed, visually assessed classification.

Half-pounder proportions were then estimated using visual classification methods described above. Estimated proportions derived from visual classifications were then compared with those based on the statistical predictions to see if there were significant differences between the results. Comparison of classification of scales according to visual and statistical (logistic regression) methods is complicated by the inherent ambiguity of statistical classifications as compared to the binary visual classifications. Therefore, two prediction cutoff ranges were used: (1) predicted probability > 0.7 (or < 0.3), and (2) predicted probability > 0.8 (or < 0.2). When predicted probabilities exceeded 0.8 (or were less than 0.2), it was assumed that statistical classifications were completely accurate. Specificity and sensitivity were both calculated to assess goodness of fit, assuming that the visual calls generated the true state of scales (Hankin et al. 2009). Sensitivity and specificity, respectively, are defined as the state classification rates for the true states, 0 or 1, where state 1 is a scale showing the half-pounder check.

<u>Estimation of Half-Pounder Proportions</u>

To develop an indicator of the tendency of steelhead to return as half-pounders, I first grouped adult steelhead by their adult age designation. For wild adult steelhead, these designations were: 1/-.1s, 2/-.1s or 3/-.1s, where the dash represents either an “h” or “1”. No annual estimates were made for life history type 3/-.1s due to small sample sizes (n = 31 total, all years). For adult hatchery steelhead (all released as age-1 smolts), the only life history type was 1/-.1s. Let n = the total number of steelhead in a particular group, and let y_i = 1 or 0 according to whether a steelhead underwent the half-pounder migration. Then, the estimated half-pounder proportion, $\hat{\pi}$, was calculated as:

$$\hat{\pi} = \sum_{i=1}^{n} \frac{y_i}{n} \quad (3)$$

The estimated half-pounder proportion may have modest positive bias as an estimator of $\sigma_{a|h}$, the probability that a fish will undergo a half-pounder migration (see Appendix A). Estimates of sampling variance of $\hat{\pi}$ were calculated using (Cochran 1977):

$$\hat{V}(\hat{\pi}) = \frac{\hat{\pi}(1-\hat{\pi})}{n-1} \quad (4)$$

Ninety-five percent confidence intervals were constructed around estimates as:

$$\hat{\pi} \pm t_{(1-\alpha,\ n-1)} * \sqrt{\hat{V}(\hat{\pi})} \quad (5)$$

Brood and Smolt Year Assignments

For each steelhead aged, a brood year and a "smolt year" were assigned in order to compare different aged steelhead (from different brood years) that shared the same ocean conditions during the first summer/fall in which they did or did not make a half-pounder run (Figure 5). For example, if a steelhead returned on its first spawning run in the fall of 1992 after spending a single winter in the ocean, then its "smolt year" was the spring/summer of 1991. Likewise, if a steelhead returned on its first spawning run in the fall of 1992, and it made a half-pounder run in the fall of 1991, then its "smolt year" would also be the spring/summer of 1991. By making these assignments, comparisons of half-pounder proportions could be made for fish with different life histories and ages.

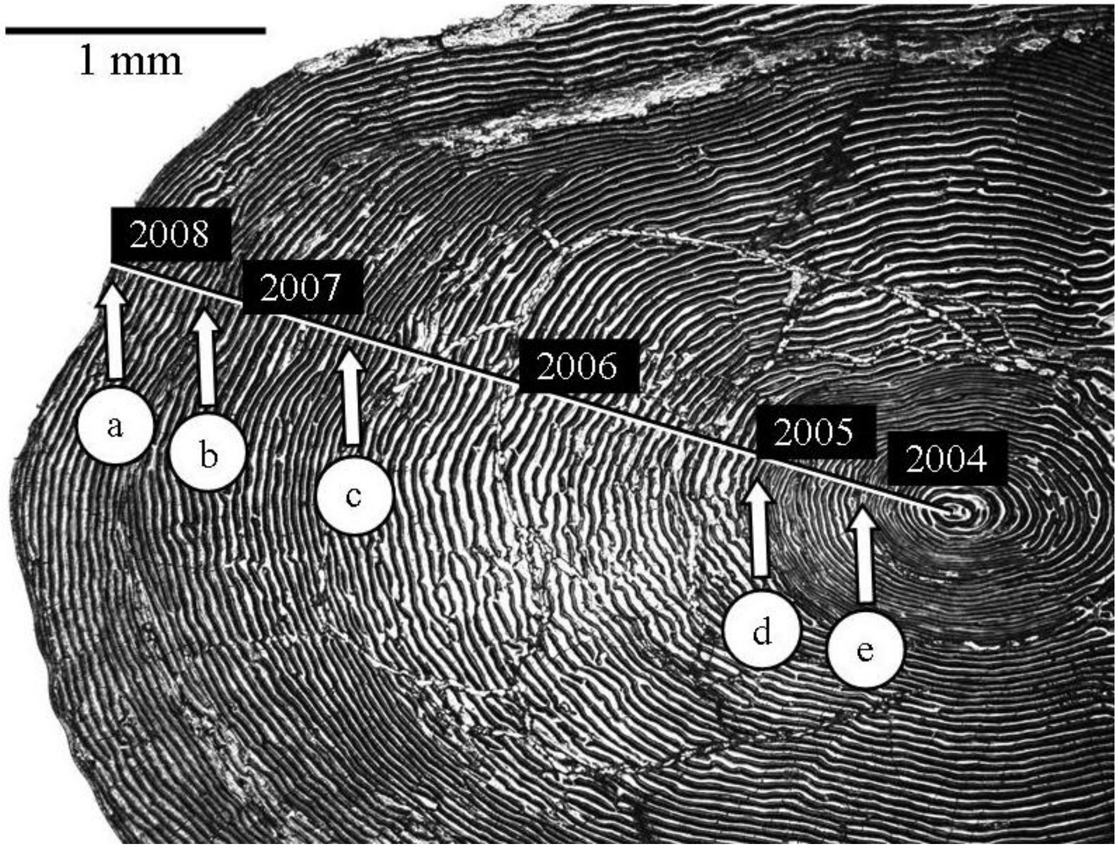

Figure 5. Image of scale from wild age-5 steelhead from Trinity River, California (670 mm FL) with life history type 2/1.2s (total age = 4+) showing life history events (a – e) and corresponding years in which they took place: (a) location of 2nd spawning run and capture during fall 2008; (b) location of spawning check during winter 2007/2008; (c) ocean annulus during winter 2006/2007; (d) location of 2nd freshwater annulus during winter 2005/2006 and; (e) location of 1st freshwater annulus in winter 2004/2005. Year assignments: brood year is 2004; smolt year is 2006.

Collection of Scale Samples

Archived scale samples collected from hatchery and wild Trinity River steelhead, from runs in 1982, 1991-1996, 2000, and 2007 were analyzed to estimate the proportions of adult steelhead exhibiting the half-pounder check. These scales had been collected at the Willow Creek weir by California Department of Fish and Game (CDFG) employees and were archived at the CDFG Office in Arcata, California. Additional contemporary scales were collected at the Willow Creek weir and Trinity River Hatchery in 2008 and 2009, and from wild and hatchery half-pounders from August 2008 to March 2009 using hook and line sampling. For every steelhead collected during contemporary collections (2008 – 2009), scale samples were taken from the left side of the fish, below the posterior margin of the dorsal fin and two scale rows above the lateral line. Fork length in centimeters was measured, sex was determined (if possible), and hatchery origin was determined from adipose fin clips. All sampling activities were covered by permits and authorizations as follows: Institutional Animal Care and Use Committee Protocol No. 07/08.F.80.A and amendments, CDFG Scientific Collecting Permit No. SC-8610, and section 10(a)(1)(A) permit #1068 modification 2.

Back-Calculations of Fork Length

A scatterplot of fish lengths at capture against scale radius exhibited both heteroscedasticity (increasing variation in lengths with increasing scale radius size) and apparent non-linearity (Figure 6). A linear body-scale relationship with appropriate constant variance was, however, achieved on a log-log scale (Bartlett et al. 1984). I used a Fraser-Lee method for back-calculation of lengths from this log-log body-scale relation:

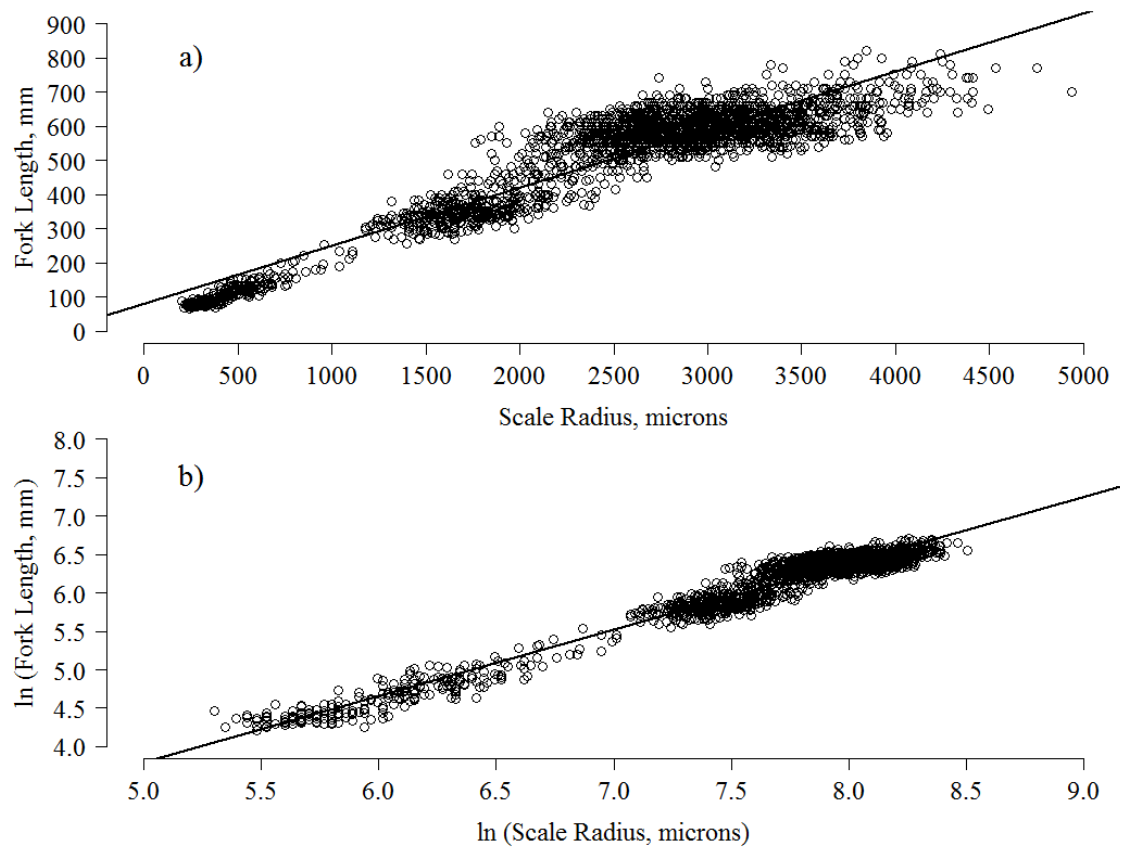

Figure 6. Relationship between the fork length (L) and scale radius (S) for all aged Trinity River steelhead (n = 2186). Note apparent non-linearity and increasing variation of lengths with increasing scale radius shown in (a). Panel (b) shows that after natural log-transformation of both L and S (b), the relationship between ln(L) and ln(S) more linear with constant variation around the least-squares fit (solid line).

$$\widehat{\ln L_i} = \hat{\alpha} + (\ln L_c - \hat{\alpha})\frac{\ln S_i}{\ln S_c} \tag{6}$$

where $\widehat{\ln L_i}$ is the estimated back-calculated fork length at time i; $\hat{\alpha}$ is the estimated intercept of the body-scale regression (in log-transformed units, i.e., ln L =$\hat{\alpha} + b \ln S$); L_c is fork length (millimeters) at capture; S_i is the distance from the scale focus to scale radius (microns) at feature i; and S_c is the scale radius (microns) at capture. Back-calculated fork lengths were calculated by exponentiating $\widehat{\ln L_i}$. Due to possible bias associated with the exponentiation of log-transformed units (Hayes et al. 1995), subsequent analyses were carried out using both exponentiated back-calculated fork lengths and non-exponentiated back-calculated fork lengths. No substantial differences in results were found, so results are presented in exponentiated back-calculated fork length units.

Back-calculated fork lengths were only calculated for steelhead prior to or on their maiden spawning run due to possible overestimation of back-calculated fork lengths resulting from scale erosion during spawning runs. Back-calculated fork lengths were only used from scales collected prior to the month of December, due to high amounts of scale erosion observed from 2009 Trinity River Hatchery collections collected during January through March. Additionally, the body-scale regression was derived from the same set of scales that met the requirements of back-calculation of fork lengths.

Statistical Analyses

Logistic regression (Stauffer 2008) was used to identify variables related to age or growth that might be associated with the presence or absence of a half-pounder check. These analyses pooled all scales samples over the years 1982 – 2009 for the two largest life history groups: hatchery origin (1/-.1s) and wild origin (2/-.1s). Covariates included in these analyses were: a) back-calculated fork length at freshwater age-1; b) back-calculated fork length at freshwater age-2; c) back-calculated fork length at the end of the freshwater zone; d) back-calculated fork length at ocean entry; and, e) age at ocean entry. Candidate models were evaluated using AIC values and AIC weights, as previously described.

Binomial tests were used to compare proportions among life history groups that all shared the same smolt year (Crawley 2007). All statistical tests, unless otherwise noted, were performed using $\alpha = 0.05$.

Welch's t-tests were used to test for differences in mean sizes of hatchery as compared to wild half-pounders collected during hook and line sampling (Welch 1947, Ruxton 2006). Change point analysis (Chen and Gupta, 1999) was used to determine if there was evidence for a statistically significant change in mean size at release for age-1 steelhead smolts from Trinity River Hatchery occurred over release years 1979 - 2007 and, if so to identify the particular year when the change occurred.

Early Marine Growth

The first 15 ocean circuli, after the point of apparent ocean entry, were measured in order to estimate mean circuli spacing for a subset of samples (n = 346). Only scales from known half-pounders captured during fall/winter 2008/2009 and adults captured during fall 2009 were used in this analysis in order to have adequate sample sizes of each life history type. It is possible that differences in early marine growth may cause slower-growing smolts to be more likely to go on a half-pounder run. Using methods similar to Beamish and Mahnken (2001) and Beamish et al. (2004), mean circuli spacing after the point of apparent ocean entry was compared between steelhead that went on a half-pounder run and those that did not.

Frequency of Multiple Spawning Events

Spawning checks are characterized by severe resorption or erosion on scale margins and a subsequent small period of scale growth indicating ocean growth (Figure 5). They are typically easily distinguishable from other life history events, as scales exhibiting only an ocean annulus do not show as much resorption along margins. The extent of apparent repeat spawning (iteroparity) among adult steelhead was tabulated by run year.

For a particular run year, the percentage of first-, second- or third-time spawners was calculated by counting all such adults on a particular spawning run and dividing by the total sample of mature adults in that run year. These percentages are, of course, affected by interannual variation in brood year survival, but they nevertheless provide a crude indicator of the incidence of repeat spawning. Kelts, steelhead that had previously spawned during the winter and were migrating to the ocean that were captured during hook and line sampling (n = 10) were not included in this analysis since they were captured after spawning and it was unknown whether or not they would survive to the next run year.

Steelhead Releases from Trinity River Hatchery

Information on numbers and mean weights of age-1 steelhead released from Trinity River Hatchery were available from annual hatchery operations reports for the years 1978/79 through 2006/07 (California Department of Fish and Game 1980 – 2007).

For a given release year, I calculated a weighted mean size at release (weight in grams) for age-1 hatchery steelhead in year i as:

$$\hat{\mu}_i = \frac{\sum_{h=1}^{L} N_h * \hat{\mu}_h}{\sum_{h=1}^{L} N_h}, \qquad (7)$$

where: L = total number of raceways holding steelhead in year i; N_h = number of fish estimated to be in raceway h $(h = 1,2,,,L)$ in year i; and, $\hat{\mu}_h$ = mean weight of steelhead in raceway h in year i. Additionally, for each release year, I determined the amount of variation in the size at release within each year and generated 95% confidence intervals for each weighted mean size at release. The calculations relied on unpublished data from Naman (2008) and sampling theory concepts that were fully developed in Appendix B.

RESULTS

Sample Sizes

A total of 2348 scale samples (combined for all years and methods of collection), including scales from 1123 adult wild steelhead and 1225 adult hatchery steelhead, were examined. Due to unreadable, ambiguous or missing scale samples, sample sizes were reduced to 1083 adult wild steelhead and 918 adult hatchery steelhead for spawning frequency analyses. Because sample exclusion criteria differed by analysis (e.g., relaxed for estimating spawning frequency but strict for estimation of half-pounder proportions), actual sample sizes for specific analyses are given in following sections as appropriate.

Quantitative Differentiation of Half-Pounder Checks versus Ocean Annuli

Scales from 607 adult steelhead were used to quantitatively differentiate half-pounder checks from ocean annuli. Logistic regression results based on AIC values and AIC weights indicated that the presence or absence of checking (Table 1, measurement #10), the total width of the first five circuli posterior to the check (Table 1,measurement #1), the coefficient of variation of the ten measurements posterior and anterior to the check (Table 1, measurement #5) and the circuli count from ocean entry to the end of the check (Table 1, measurement #6) were associated with the half-pounder check. The top five models all included both measurements #1 and #10 (Table 2).

The top model based on AIC weights, model #26 with all steelhead included, had 93.70% overall accuracy, meaning that individual classifications (i.e., half-pounder check or not) from visual and quantitative classifications were in agreement 93.70% (569 correct / 607 total) of the time (Table 3). Accuracy of models 26, 27, and 25

Table 2. Top five models (of thirty candidate models) and null model based on AIC and AIC weights to quantitatively distinguish between half-pounder checks and ocean annuli from scale analysis of adult steelhead scales.

Model Name	AIC	Parameters	Model Likelihood	AIC Weights	ΔAIC
26	126.651	10, 1, 5	1.000	0.825	0.000
27	130.197	10, 1, 6	0.170	0.140	3.546
25	133.597	10, 1, 4	0.031	0.026	6.946
28	135.851	10, 1, 8	0.010	0.008	9.200
10	140.290	10, 1	0.001	0.001	13.639
Null	518.453	None	0.000	0.000	391.802

Parameter definitions: 1 = Total width of the first five circuli inside suspected check; 4 = Mean width of the first five circuli outside suspected check; 5 = Coefficient of variation of ten measurements inside and outside of suspected check; 6 = Circuli count from apparent ocean entry to end of suspected check; 8 = Ratio of measurement 1/measurement 2; 10 = Presence or absence of checking along scale margin near suspected check (likely indicating freshwater residence)

Table 3. Goodness of fit (using leave-one-out) values for top three candidate models to differentiate between half-pounder checks and ocean annuli. For each model, three exclusion criteria were used: 1) None (no steelhead excluded); 2) only steelhead with predicted probabilities P>0.7 (or P<0.3) included, and; 3) only steelhead with predicted probabilities P>0.8 (or P<0.2) included.

						Estimated Half-Pounder Proportions			
Model #	AIC	AIC weight	Exclusion Criteria	n	Accuracy	Visual	Model	Sensitivity	Specificity
26	126.651	0.825	None	607	0.937	0.152	0.133	0.728	0.975
			P>0.7 (or P<0.3)	561	0.968	0.128	0.111	0.806	0.992
			P>0.8 (or P<0.2)	534	0.978	0.112	0.094	0.817	0.998
27	130.197	0.140	None	607	0.932	0.152	0.145	0.761	0.963
			P>0.7 (or P<0.3)	552	0.971	0.116	0.098	0.797	0.994
			P>0.8 (or P<0.2)	531	0.977	0.102	0.083	0.796	0.998
25	133.597	0.026	None	607	0.931	0.152	0.122	0.674	0.977
			P>0.7 (or P<0.3)	563	0.952	0.126	0.103	0.718	0.986
			P>0.8 (or P<0.2)	527	0.975	0.108	0.091	0.807	0.996

all increased with increasingly strict criteria for exclusion of scales with "ambiguous" statistical classification. Overall accuracy ranged from 97.5% to 97.8% for classification probabilities exceeding 0.8 (or less than 0.2). Specificity, the correct classification rate for non-half-pounders (model predicts 0 when visual call or true state = 0) increased with increasingly strict criteria for exclusion of scales, but even for the top model (model #26) only increased to 0.817. Sensitivity, on the other hand, was high for all three top models and for all exclusion criteria, becoming nearly 100% for classification probabilities exceeding 0.8 (or less than 0.2) (Table 3).

Estimates of half-pounder proportions derived by the visual classification method were consistently higher than the statistical classification method and ranged from 4.35% higher to 19.57% higher (Table 3). The range represents a misclassification rate of about 1 misclassification every 152 scales examined to about 1 misclassification every 34 scales examined.

Estimated Half-Pounder Proportions during Study Period

Estimates of half-pounder proportions were based on 693 adult wild steelhead and 867 adult hatchery steelhead for which assignments of life history type were judged extremely accurate. Among age-2 wild adult steelhead that spent two summers in the ocean and that were first-time spawners (1/h.1s or 1/1.1s), estimated half-pounder proportions ranged from 0.00 (2007) to 1.00 (1982) (Figure 7). Confidence intervals constructed around estimated proportions were quite large for some smolt years with small sample sizes ($n < 10$), however (Figure 7).

Among age-3 wild adult steelhead that spent two summers in the ocean and that were first-time spawners (2/h.1s or 2/1.1s), estimated half-pounder proportions ranged

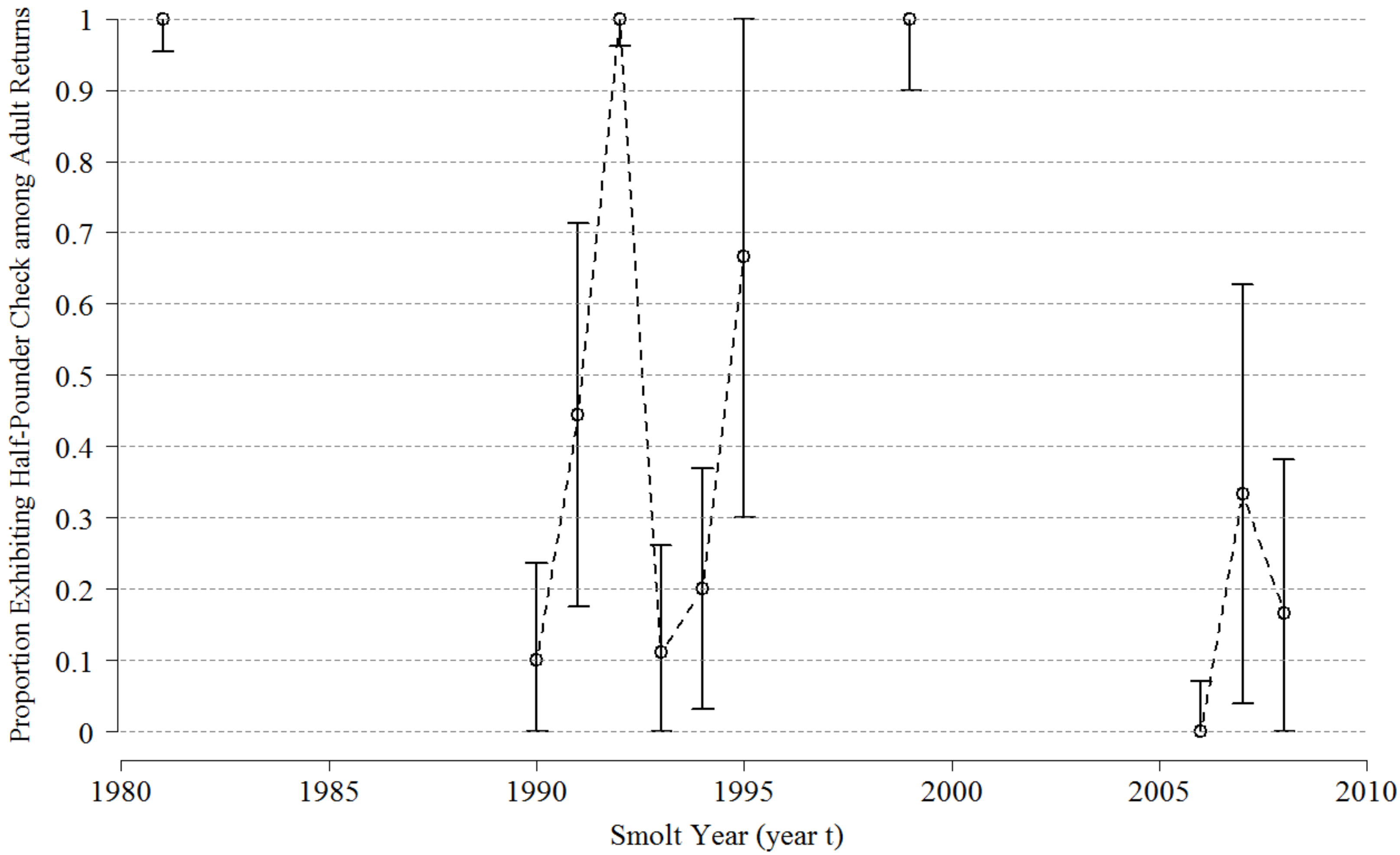

Figure 7. Half-pounder proportions over study period for wild steelhead adults (age-1 at ocean entry – open circles) in life history group 1/-.1s with 95% confidence intervals around estimated proportion.

from about 0.020 (smolt years 1993, 2006 and 2007) to 0.714 (smolt year 1981) (Figure 8). Estimated proportions for the remaining years were generally low, typically below 0.20, with the exception of smolt years in 1981 and 1999. Among age-4 wild adult steelhead (n = 31 for all sample years) that spent two summers in the ocean and that were first-time spawners (3/h.1s or 3/1.1s), only two had returned previously on a half-pounder run.

Among age-2 hatchery adult steelhead that spent two summers in the ocean and that were first-time spawners (1/h.1s or 1/1.1s), estimated half-pounder proportions ranged from 0.00 (smolt years 1990 and 2006) to 0.750 (smolt year 1981) (Figure 9). For wild steelhead that returned as age-2 adults (1/-.1s) that entered the ocean in 1981, 1992 and 1999, estimated half-pounder proportions were higher than all other years. With the exception of smolt years 1981, 1992 and 1999, half-pounder proportions among returning wild adults (1/-.1s) were typically less than 0.400. For wild steelhead that returned as age-3 adults (2/-.1s) that entered the ocean in 1981 and 1999, estimated half-pounder proportions were higher than all other years. With the exception of 1981 and 1999, half-pounder proportions among returning wild adults (2/-.1s) were typically less than 0.200. For hatchery steelhead that returned as age-2 adults (1/-.1s) that entered the ocean in 1981, 1991 and 1992, estimated half-pounder proportions were higher than all other years. With the exception of 1981, 1991 and 1992, half-pounder proportions among returning hatchery adults (1/-.1s) were typically less than 0.150.

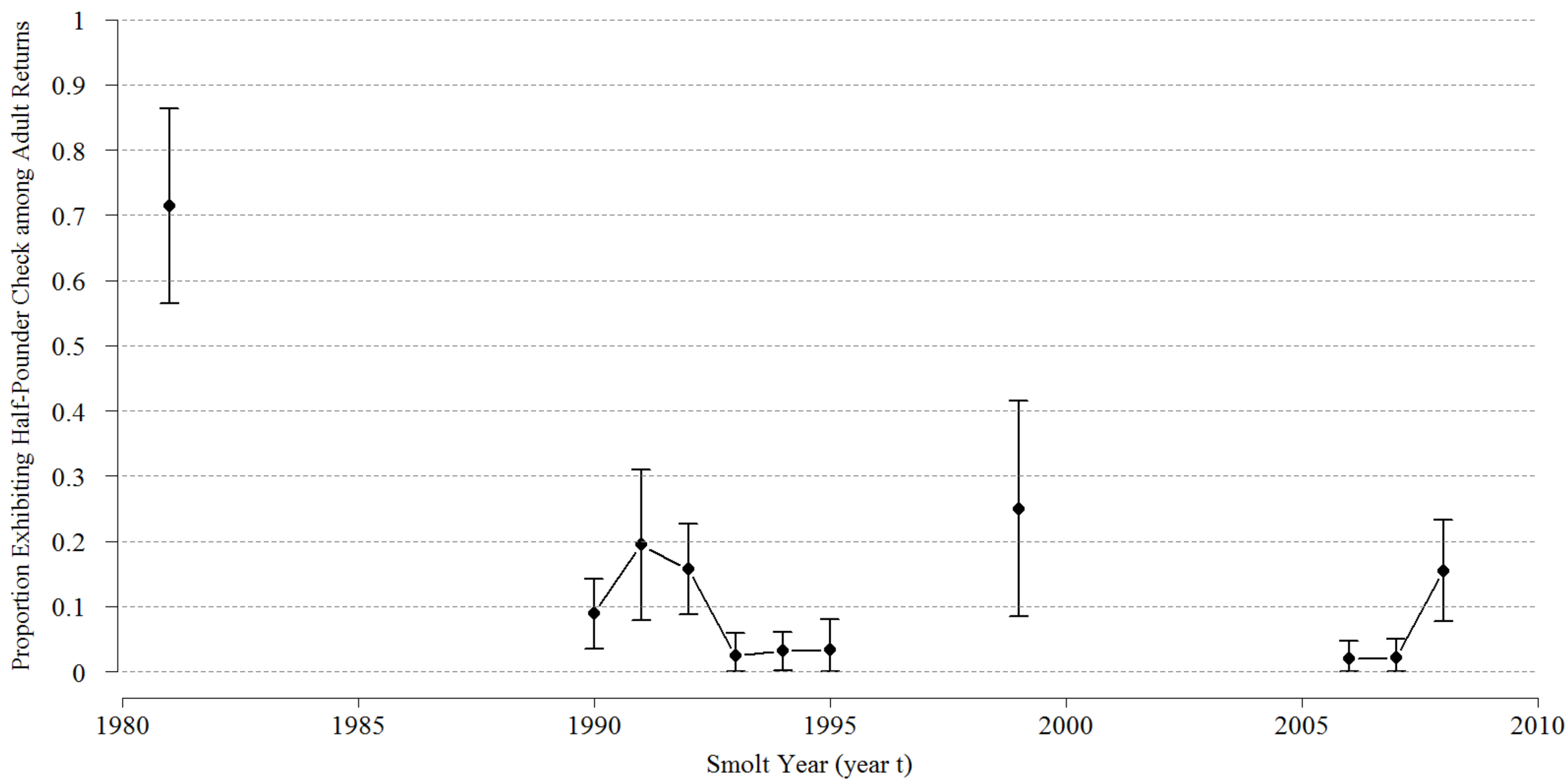

Figure 8. Half-pounder proportions over study period for wild steelhead adults (age-2 at ocean entry – closed circles) in life history group 2/-.1s with 95% confidence intervals around estimated proportion.

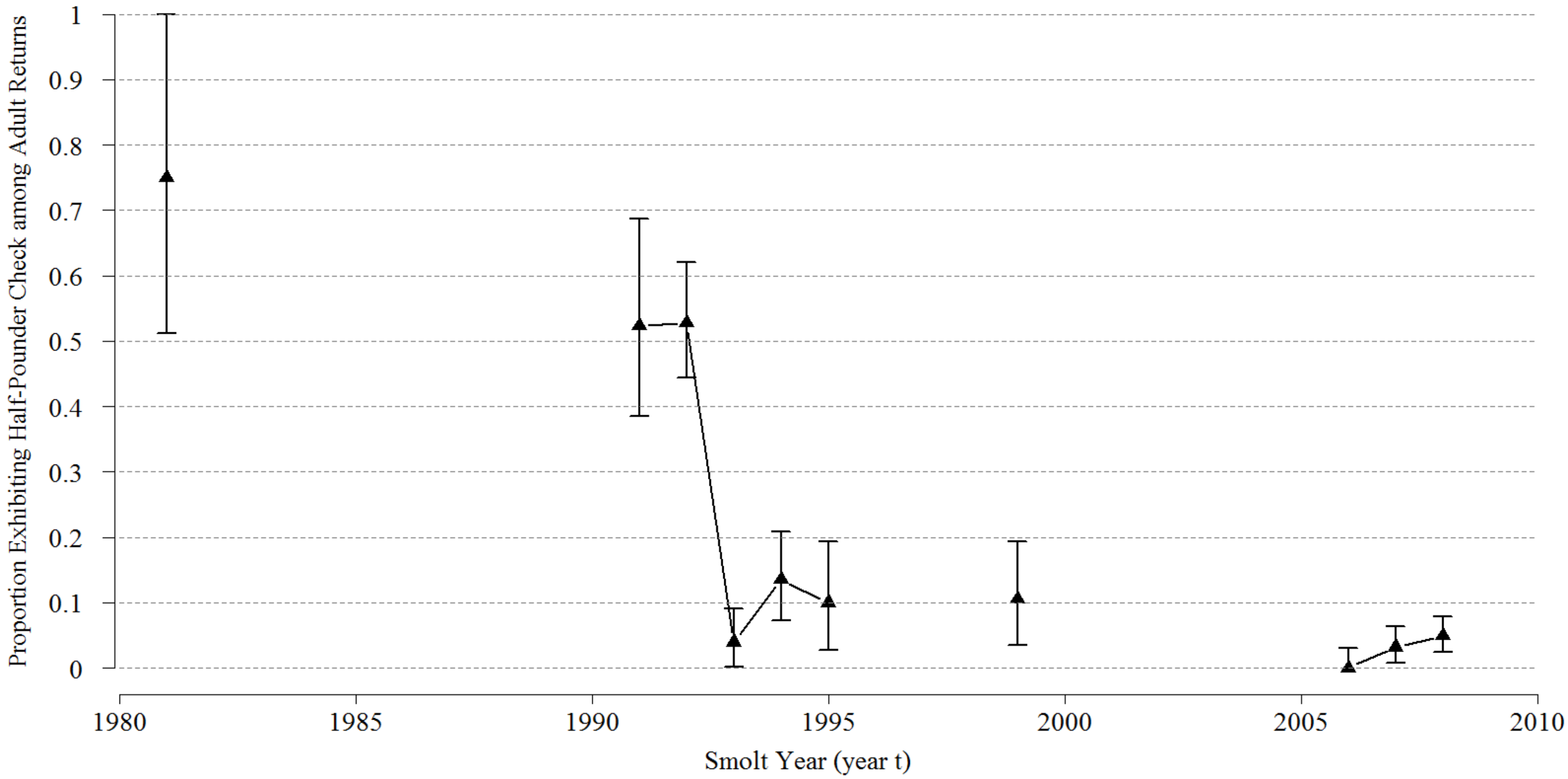

Figure 9. Half-pounder proportions over study period for hatchery steelhead adults (age-1 at ocean entry – closed triangles) in life history group 1/-.1s with 95% confidence intervals around estimated proportion. No estimate was made for smolt year 1990 as only two samples from hatchery steelhead adults were available for that particular year.

Comparison of Half-Pounder Proportions

Results from two-tailed binomial tests comparing proportions among life history groups from the same smolt years indicated that hatchery steelhead entering the ocean after one freshwater year had significantly higher half-pounder proportions than wild steelhead that spent two years in freshwater in three out of seven smolt years prior to 1995: 1991 ($P = 0.006$), 1992 ($P = <0.001$) and 1994 ($P = 0.020$) (Table 4). In contrast, in smolt year 2008, wild steelhead that spent two years in freshwater had a significantly higher half-pounder proportion than hatchery steelhead entering the ocean after one freshwater year ($P=0.006$). Wild steelhead entering the ocean after spending only one year in freshwater had significantly higher half-pounder proportions than wild steelhead that spent two years in freshwater in four out of eleven smolt years: 1992 ($P = <0.001$), 1995 ($P= 0.010$), 1999 ($P = 0.010$) and 2007 ($P = 0.027$) (Table 4). In all but one sampled smolt year, half-pounder proportions for age-1 smolts were greater than those for age-2 smolts.

Results from binomial tests of pooled proportions across two periods indicated that estimated proportions were significantly higher for all life history types during the early period (smolt years 1981, 1990-1992) than during the late period (1993-1995, 1999, 2006-2008) (Table 4). For hatchery steelhead with life history type 1/-.1s, half-pounder proportions were significantly higher during the early period than the late period (binomial test, one-tailed, $P < 0.001$). Half-pounder proportions were significantly higher during the early period than the late period for wild steelhead with life history types 1/-.1s (binomial test, one-tailed, $P < 0.001$) and significantly higher for life history type 2/-.1s (binomial test, one-tailed, $P < 0.001$).

Table 4. Counts and proportions of half-pounder checks among returning first-time spawning adults (adult ages 2+ and 3+) in year t+1 among Trinity River steelhead by age at ocean entry and origin.

	Hatchery			Wild					
	Age-1 at Ocean Entry			Age-1 at Ocean Entry			Age-2 at Ocean Entry		
Smolt Year	Half-Pounder Check(s)	Total	Proportion	Half-Pounder Check(s)	Total	Proportion	Half-Pounder Check(s)	Total	Proportion
1981	6	8	0.750	11	11	1.000	20	28	0.714
1990	0	2	0.000	1	10	0.100	8	90	0.089
1991	22	42	0.524[b]	4	9	0.444	7	36	0.194[b]
1992	65	123	0.528[a,b]	13	13	1.000[a,c]	14	89	0.157[b,c]
Pooled Proportions 1981-1992			0.531[b,d]			0.674[c,d]			0.202[b,c,d]
1993	3	75	0.040	1	9	0.111	1	41	0.023
1994	13	96	0.135[b]	3	15	0.200	3	95	0.032[b]
1995	5	50	0.100	2	3	0.667[c]	1	30	0.033[c]
1999	6	57	0.105[a]	5	5	1.000[a,c]	5	20	0.250[c]
2006	0	16	0.000	0	7	0.000	1	51	0.020
2007	5	154	0.032[a]	2	6	0.333[a,c]	1	48	0.021[c]
2008	12	244	0.049[b]	1	6	0.167	11	71	0.155[b]
Pooled Proportions 1993-2008			0.064[a,d]			0.275[a,c,d]			0.065[c,d]

[a] Significant difference (two-tailed, binomial test) between proportions of adult age-2+ hatchery and adult age-2+ wild steelhead; [b] Significant difference (two-tailed, binomial test) between proportions of adult age-2+ hatchery and adult age-3+ wild steelhead; [c] Significant difference (two-tailed, binomial test) between proportions of adult age-2+ wild and adult age-3+ wild steelhead; [d] Significant difference (one-tailed, binomial test) between proportions of early period (smolt years 1981, 1990-1992) and late period (smolt years 1993-1995, 1999, 2006-2008).

Back-Calculated Fork Lengths

A strong linear relationship was found between the natural logarithms of fork length and scale radius (Figure 6) when all data were pooled across all years ($R^2 = 0.956$, n = 2186). The fitted body-scale relationship in (natural log-transformed units) was: $\ln(L) = -0.5037 + 0.8609 \ln(S)$.

Logistic Regression Analyses

All wild steelhead that entered the ocean after two years in freshwater were pooled across all years (n = 479). Due to the high inter-annual variation in half-pounder proportions, smolt year was included as a factor and allowed to interact with back-calculated fork lengths to explain the presence or absence of a half-pounder check. The model (#27) which included the interaction between smolt year and back-calculated length at the end of the freshwater zone was the top model (Table 5). Based on AIC values and weights, top models in this analysis included back-calculated fork length at the end of the freshwater zone and smolt year.

All wild steelhead, freshwater life history types 1, 2 or 3 at ocean entry, were pooled across years (n = 587). Table 6 summarizes candidate models to explain presence or absence of a half-pounder check among the life history groups a/-.1s. Based on AIC values and AIC weights, two models appeared to be useful in explaining the occurrence of a half-pounder check. The two top models, model #31 (AIC = 371.17) and model #27 (AIC = 371.57), both contained size at the end of freshwater zone and the year of ocean entry. Model #31 also included age at ocean entry. Year of ocean entry appeared as a variable in the top nine models in this analysis. For wild steelhead, several variables appear to be associated with the presence or absence of a half-pounder check.

Table 5. Summary of binary logistic regression models ranked on AIC and AIC weights to explain occurrence of the half-pounder run (life history type 2/h.1s) among individual steelhead that migrated to ocean as age-2 smolts (n = 479) with smolt year interaction (treated as a factor) in the analysis.

Model name	AIC	Parameters	Model Likelihood	AIC Weights	ΔAIC
27	304.28	BCENDFW * YEAR	1.000	0.435	0.000
18	305.44	BCENDFW, YEAR	0.562	0.244	1.154
17	306.28	BCFW2, YEAR	0.369	0.160	1.996
26	306.29	BCFW2 * YEAR	0.367	0.160	2.005
19	319.29	BCOE, YEAR	0.001	0.000	15.003
28	321.31	BCOE * YEAR	0.000	0.000	17.025
3	357.45	BCENDFW	0.000	0.000	53.161
2	357.95	BCFW2	0.000	0.000	53.668
4	375.78	BCOE	0.000	0.000	71.492
Null	382.40	None	0.000	0.000	78.117

* BCFW2 = back-calculated fork length at second freshwater annulus; BCENDFW = back-calculated fork length at end of freshwater zone; BCOE = back-calculated fork length at ocean entry; YEAR = smolt year (year of ocean entry).

Table 6. Summary of top three binary logistic regression models (out of 36 candidate models) and null model, ranked on AIC and AIC weights to explain occurrence of the half-pounder run (among all life history types a/h.1s) among individual steelhead that migrated to ocean as age-1, age-2 or age-3 smolts (n = 587).

Model name	AIC	Parameters	Model Likelihood	AIC Weights	ΔAIC
31	371.17	BCENDFW, YEAR, AGEOE	1.000	0.457	0.00
27	371.57	BCENDFW, YEAR	0.818	0.374	0.40
35	373.17	BCFW1, BCENDFW, YEAR	0.369	0.169	2.00
Null	537.88	None	0.000	0.000	166.70

* BCFW1 = back-calculated fork length at first freshwater annulus; BCENDFW = back-calculated fork length at end of freshwater zone; AGEOE = age at ocean entry; YEAR = smolt year (year of ocean entry).

Top models in both analyses presented in Tables 5 and 6 contain the back-calculated fork length at the end of the freshwater zone as well as smolt year. The top model in Table 6 contains both of these variables in addition to age at ocean entry.

All hatchery steelhead that were released as one-year old smolts were pooled across all years (n = 741). The model that included the single parameter, smolt year, was by far the strongest model according to AIC and AIC weights (0.997) (Table 7). A similar analysis was conducted using estimated mean weight of steelhead releases from Trinity River Hatchery from 1981 to 2007 (n = 497). Data from 2008 and 2009 were not included in this analysis because release data for those particular years was not available. The variable mean weight of release was in four of the top five models (Table 8) and negatively affected the probability of a half-pounder check in the four models that included it.

Half-pounder Lengths at Capture

Scale samples were also available from 244 known half-pounders captured from August 2008 through March 2009 (wild = 110, hatchery = 134). Four of these samples were excluded from further analysis due to unreadable scales. The mean monthly fork lengths for both wild and hatchery half-pounders captured with hook and line sampling increased gradually over the winter, suggesting that a modest amount of growth (40-50 mm fork length) occurred during the freshwater residence of half-pounders (Figures 10, 11). This was also corroborated when I measured the mean difference of fork lengths at time of capture (observed half-pounder lengths) and at the end of the freshwater migration (anterior end of the half-pounder check back-calculated from adult scales). Although a crude measure, the mean difference for wild fish was 36 mm and mean

Table 7. Summary of binary logistic regression models ranked on AIC and AIC weights to explain occurrence of the half-pounder run (life history type 1/h.1s) among individual hatchery steelhead that migrated to ocean as age-1 smolts (n = 741) with smolt year and clip type treated as a factors in the analysis.

Model name	AIC	Parameters	Model Likelihood	AIC Weights	ΔAIC
3	500.62	YEAR	1.000	0.997	0.00
4	512.20	BCOE, YEAR	0.003	0.003	11.58
5	574.60	CLIP	0.000	0.000	73.98
1	652.51	BCOE	0.000	0.000	151.89
Null	661.62	None	0.000	0.000	161.00

* BCOE = back-calculated fork length at ocean entry; YEAR = smolt year (year of release); CLIP = clip type (i.e. AD, RV, LV, etc.).

Table 8. Summary of logistic regression models ranked on AIC and AIC weights to explain occurrence of the half-pounder run (life history type 1/h.1s) among individual hatchery steelhead that migrated to ocean as age-1 smolts (n = 497) with smolt year and clip type treated as a factors in the analysis. Releases from 2008 were not included in analysis.

Model name	AIC	Parameters	Model Likelihood	AIC Weights	ΔAIC
9	399.15	MEANWT, YEAR, BCOE	1.000	0.867	0.00
8	402.92	MEANWT, YEAR	0.152	0.132	3.77
4	412.66	BCOE, YEAR, BCOE*YEAR	0.001	0.001	13.51
7	450.92	MEANWT, BCOE	0.000	0.000	51.78
6	456.35	MEANWT	0.000	0.000	57.21
5	478.56	CLIP	0.000	0.000	79.41
1	505.15	BCOE	0.000	0.000	106.00
Null	524.88	None	0.000	0.000	125.73

* BCOE = back-calculated fork length at ocean entry; YEAR = smolt year (year of release); CLIP = clip type (i.e. AD, RV, LV, etc.), MEANWT = estimated mean weight of TRH releases for sample years 1981 – 2007.

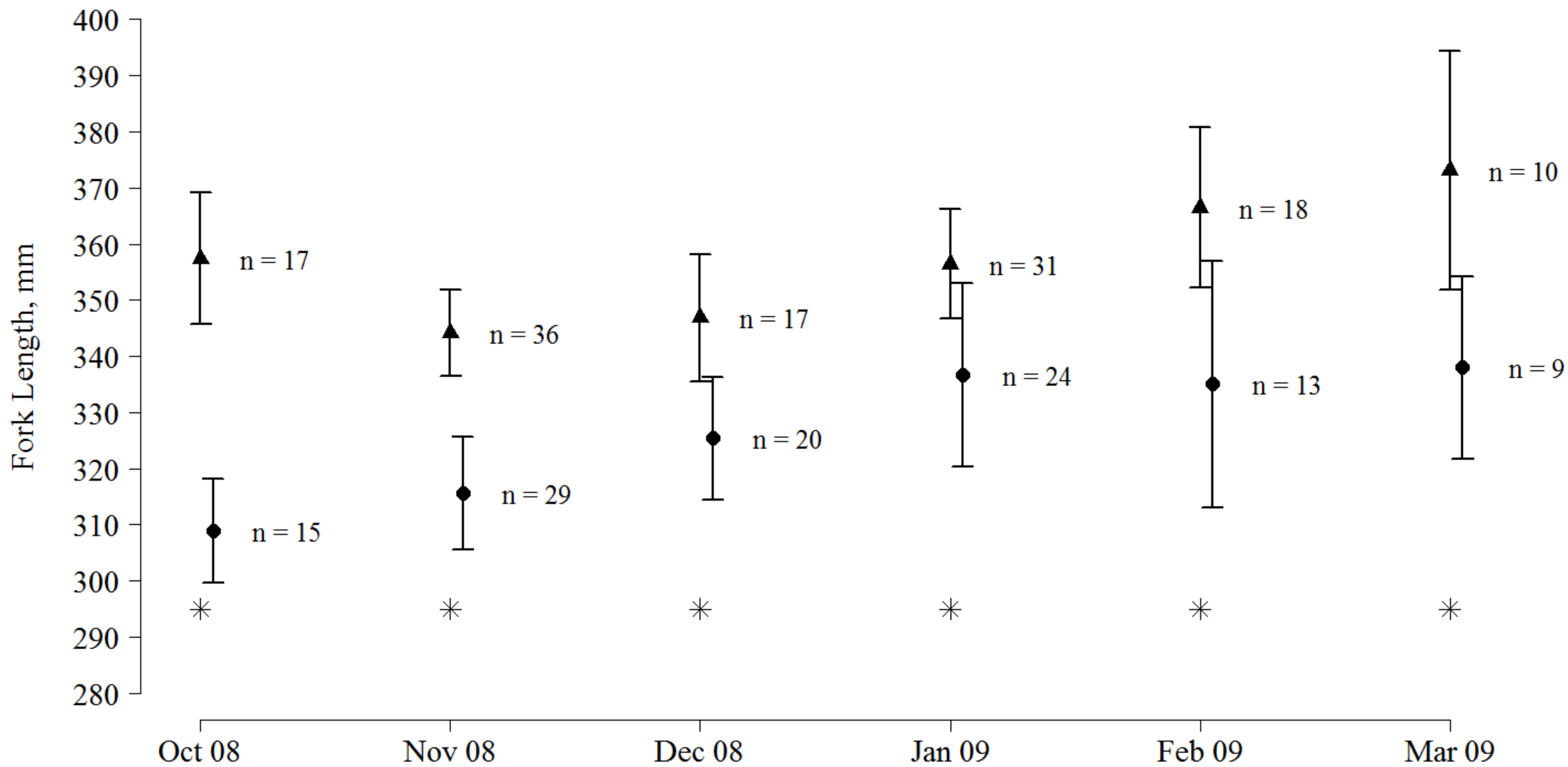

Figure 10. Monthly mean fork lengths and confidence intervals of hatchery (solid triangles) and wild (solid circles) half-pounders captured during hook and line sampling on Lower Trinity River winter 2008/2009. Asterisk denotes significant differences in mean monthly fork length.

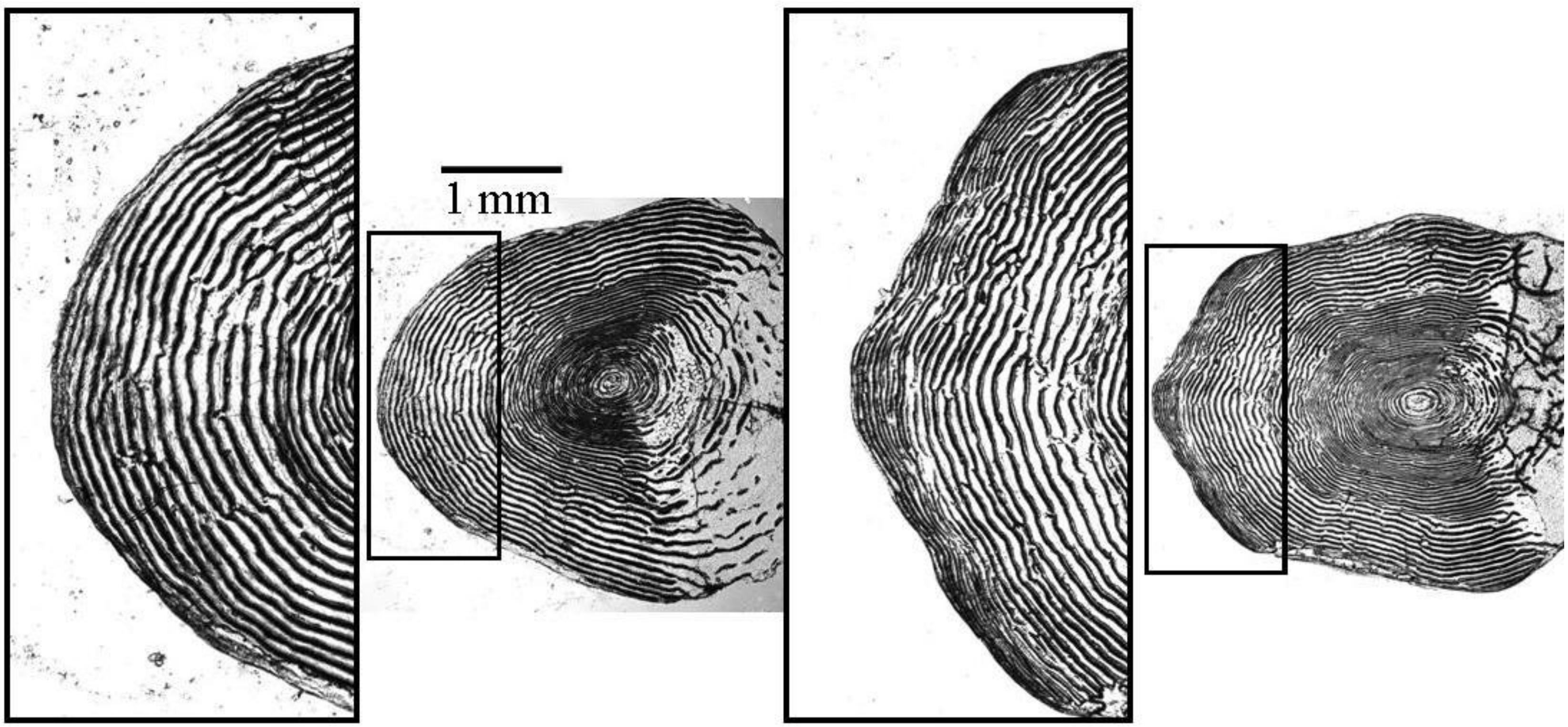

Figure 11. Pairs of images of scales from two half-pounder steelhead from Trinity River, California. Left pair: Life history type 1/h captured 18 October 2008 (330 mm) and showing little or no evidence of half-pounder check; right pair: life history type 2/h captured 3 December 2008 showing formation of half-pounder check (353 mm) during freshwater residence.

difference for hatchery steelhead was 66 mm. For every month of collection in fall 2008 through winter 2009 (October 2008 – March 2009), mean fork lengths of hatchery half-pounders significantly ($P < 0.05$) exceeded those of wild half-pounders (Figure 10). A similar size difference was also found with more limited hook and line sampling during fall 2009 (mean fork length for hatchery half-pounders was 350.4 mm, n = 10 compared to 314.0 mm, n = 17, for wild half-pounders).

Back-calculated lengths at freshwater reentry

For every steelhead (half-pounders and adults) that went on a half-pounder run, the back-calculated fork length at the beginning of the half-pounder run was calculated (Table 9). Figure 12 shows length-frequency histograms of back-calculated fork lengths at the beginning of the half-pounder check (freshwater entry in fall 2008), at the end of the half-pounder check (winter 2008/2009), and actual observed half-pounder lengths at capture (winter 2008/2009). In most years both the back-calculated fork lengths at the beginning of half-pounder run (data from half-pounders and adults that exhibited half-pounder runs) and observed half-pounder lengths of hatchery steelhead are larger (several centimeters) than wild half-pounders.

Early Marine Growth

Among wild adult steelhead captured at Willow Creek weir in fall 2009 that were smolt age-2 at ocean entry (life history types 2/h.1s or 2/1.1s), mean circuli spacing of the first 15 ocean circuli was not significantly different for the 16 steelhead that exhibited a half-pounder check than for 66 steelhead that did not (Welch’s t-test, P = 0.200, df = 11.097) (Figure 13). Among hatchery adult steelhead that were age-1 smolts at ocean

Table 9. Back-calculated fork lengths (mm) at beginning of half-pounder runs by age at ocean entry and origin, smolt years 1980 - 2008. Data based on back-calculations from collected scales of adults exhibiting half-pounder runs and from observed half-pounders.

	Wild				Hatchery	
	Age-1		Age-2		Age-1	
Year	n	Mean Fork Length	n	Mean Fork Length	n	Mean Fork Length
1980	0	NA	3	362.09	0	NA
1981	9	349.48	18	377.51	5	384.19
1982	0	NA	0	NA	0	NA
1989	5	364.40	4	342.82	1	376.68
1990	0	NA	7	374.17	0	NA
1991	4	316.00	12	337.98	18	370.45
1992	21	347.95	21	364.36	70	388.69
1993	2	371.29	2	396.88	11	363.00
1994	8	334.31	10	363.77	15	419.03
1995	4	398.78	2	363.29	19	378.21
1996	0	NA	3	440.97	0	NA
1998	3	308.93	2	355.15	2	405.23
1999	5	360.61	4	357.24	3	402.62
2000	0	NA	0	NA	6	379.95
2005	0	NA	1	346.28	0	NA
2006	0	NA	1	271.23	0	NA
2007	2	333.37	2	355.79	3	367.84
2008	34	295.10	91	318.55	152	339.82

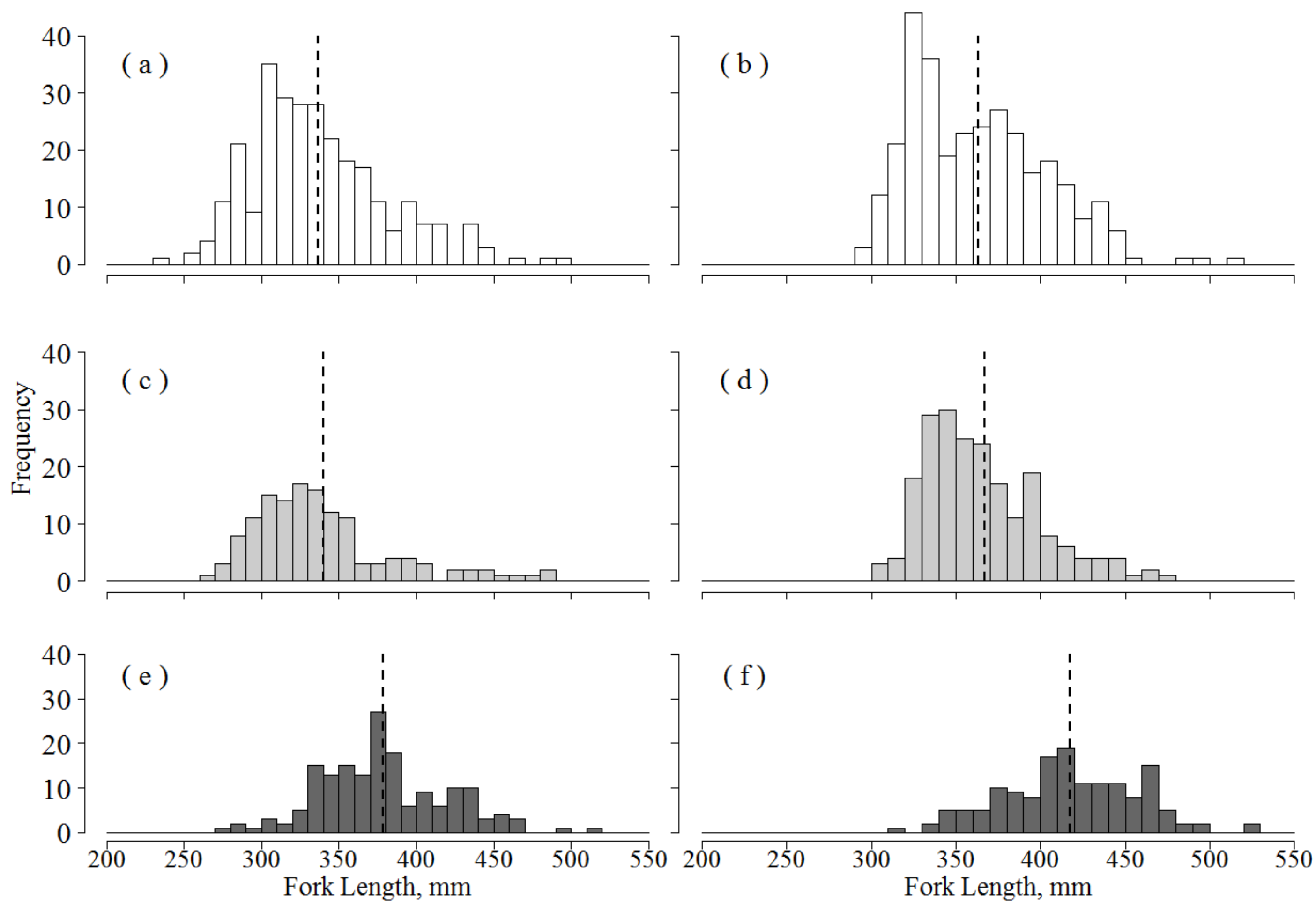

Figure 12. Histograms of back-calculated fork lengths (mm) from wild adult steelhead (panels: a, c, e) at freshwater re-entry (white bars) (all years combined), at the apparent end of half-pounder migration (dark gray bars) (all years combined), and observed half-pounder fork lengths (winter 2008-2009 only) (light gray bars). Hatchery steelhead shown in panels b, d, and f. Dashed vertical lines represent mean fork lengths.

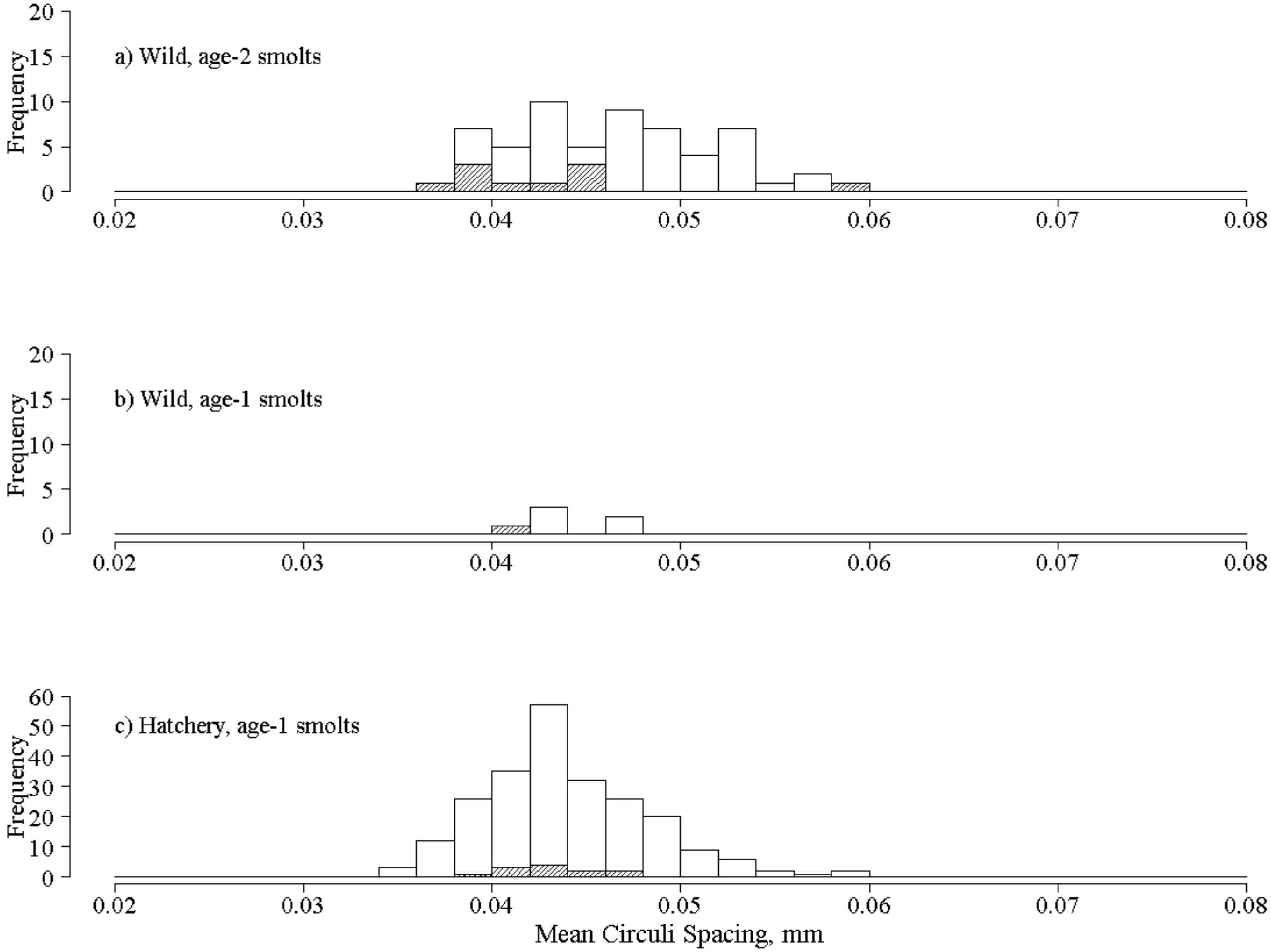

Figure 13. Mean circuli spacing, mm, for the first 15 ocean circuli from adult steelhead captured at the Willow Creek Weir during fall 2009. Spacing measured from adult scales with half-pounder checks are shown in gray; spacing from scales with ocean annuli are shown in white.

entry (life history types 1/h.1s or 1/1.1s) captured at Willow Creek weir in fall 2009, no significant differences were detected between the mean circuli spacing of the two groups ($P = 0.299$, $df = 14.328$).

Frequency of Multiple Spawning Events

Among all aged wild adult steelhead, almost all (993/1083 = 91.7%) were on their maiden spawning run (Table 10). About 7.5% (81/1083) of adult steelhead were on a second spawning run, and about 0.8% (9/1083) were on a third spawning run. Among all aged hatchery adult steelhead, 96.2% (883/918) were on their maiden spawning run, about 3.8% were on their second spawning run. None were on a third spawning run. Results from a binomial test comparing these proportions ($\alpha = 0.05$) indicate that the proportion of repeat spawners among wild adult steelhead was higher than for hatchery steelhead (all run years combined, $P < 0.001$).

Unique Life Histories

Seventeen unique and identifiable life histories were determined by scale analysis for wild and hatchery steelhead combined over the study period (Table 11). Two additional life histories were apparent from several adults on their third spawning run, but freshwater years could not be identified for these two adults (e.g., life history designations were NA/h.3s and NA/1.3s).

Among hatchery adult steelhead, the most common life history type was 1/1.1s (73.1% of total) and the second-most common life history type was 1/h.1s (14.8% of total). Among wild adult steelhead, the most common life history type was 2/1.1s (61.3% of total) and the second-most common life history type was 2/h.1s (9.0% of total).

Table 10. Number of first-, second- and third-time spawners among wild and hatchery steelhead among all aged Trinity River scale samples (1982 - 2009).

	Wild			Hatchery		
Run Year	First	Second	Third	First	Second	Third
1982	46	4	0	8	1	0
1991	139	7	1	13	1	0
1992	69	17	0	54	1	0
1993	144	1	0	124	0	0
1994	137	6	0	84	0	0
1995	174	4	0	114	0	0
1996	25	3	0	29	0	0
2000	44	13	0	60	6	0
2007	74	11	5	17	1	0
2008	68	7	1	197	24	0
2009	73	8	2	183	1	0
Totals	993	81	9	883	35	0

Table 11. Unique and identifiable life histories and numbers of each life history exhibited by wild (n = 829) and hatchery (n = 986) steelhead in the Trinity River as determined by scale analysis and corresponding life history designations. Two additional unique but not fully identifiable life histories were observed among several adults on third spawning runs, but with unclear freshwater life histories.

Wild						Hatchery	
Age-1 Smolts		Age-2 Smolts		Age-3 Smolts		Age-1 Smolts	
LH Type	Number	LH Type	Number	LH Type	Number	LH Type	Number
1/1.1s	53	2/1.1s	508	3/1.1s	32	1/1.1s	721
1/h.1s	46	2/h.1s	75	3/h.1s	2	1/h.1s	145
1/1.2s	3	2/1.2s	40	3/1.2s	5	1/1.2s	33
1/h.2s	2	2/h.2s	11	3/2.1s	1	1/h.2s	1
1/2.1s	5	2/2.1s	18			1/2.1s	75
1/h.1.1s	13	2/h.1.1s	14			1/h.1.1s	11
		2/h.1.2s	1				
Totals	122		667		40		986

Size at Return of Adult Steelhead

The size at return (observed fork length at return) of life history type a/1.1s (no half-pounder run, on first adult spawning run) for both wild and hatchery steelhead was typically 60-80 mm larger than the life history type a/h.1s (half-pounder run, on first adult spawning run) (Figure 14). Results from Welch's t-tests indicated that observed mean fork lengths of steelhead of life history type a/1.1s were significantly larger (60-80 mm) than steelhead of life history type a/h.1s ($P < 0.001$) for wild steelhead with life history types 1/-.1s and 2/-.1s and for hatchery steelhead with life history type 1/-.1s. Mean fork length of wild adult steelhead of life history type 1/1.1s was 584 mm as compared to 504 mm for life history type 1/h.1s. Mean fork length of wild adult steelhead of life history type 2/1.1s was 601 mm as compared to 522 mm for life history type 1/h.1s. Mean fork length of hatchery adult steelhead of life history type 1/1.1s was 608 mm as compared to 550 mm for life history type 1/h.1s.

The larger size of older smolts at ocean entry appeared to carry though to adult size. For adults that remained in the ocean during the first ocean winter and had been age 1 smolts (life history type 1/1.1s), mean fork length was 586 mm. This is significantly smaller ($P = 0.005$, $df = 63.0$) than mean fork length (601 mm) of adults that had been age 2 smolts (life history type 2/1.1s) For adults that went on a half-pounder migration and had been age 1 smolts (life history type 1/h.1s) , mean fork length was 504 mm, significantly ($P = 0.026$, $df = 80.9$) smaller than mean fork length (522 mm) of adults that had been age 2 smolts (life history type 2/h.1s).

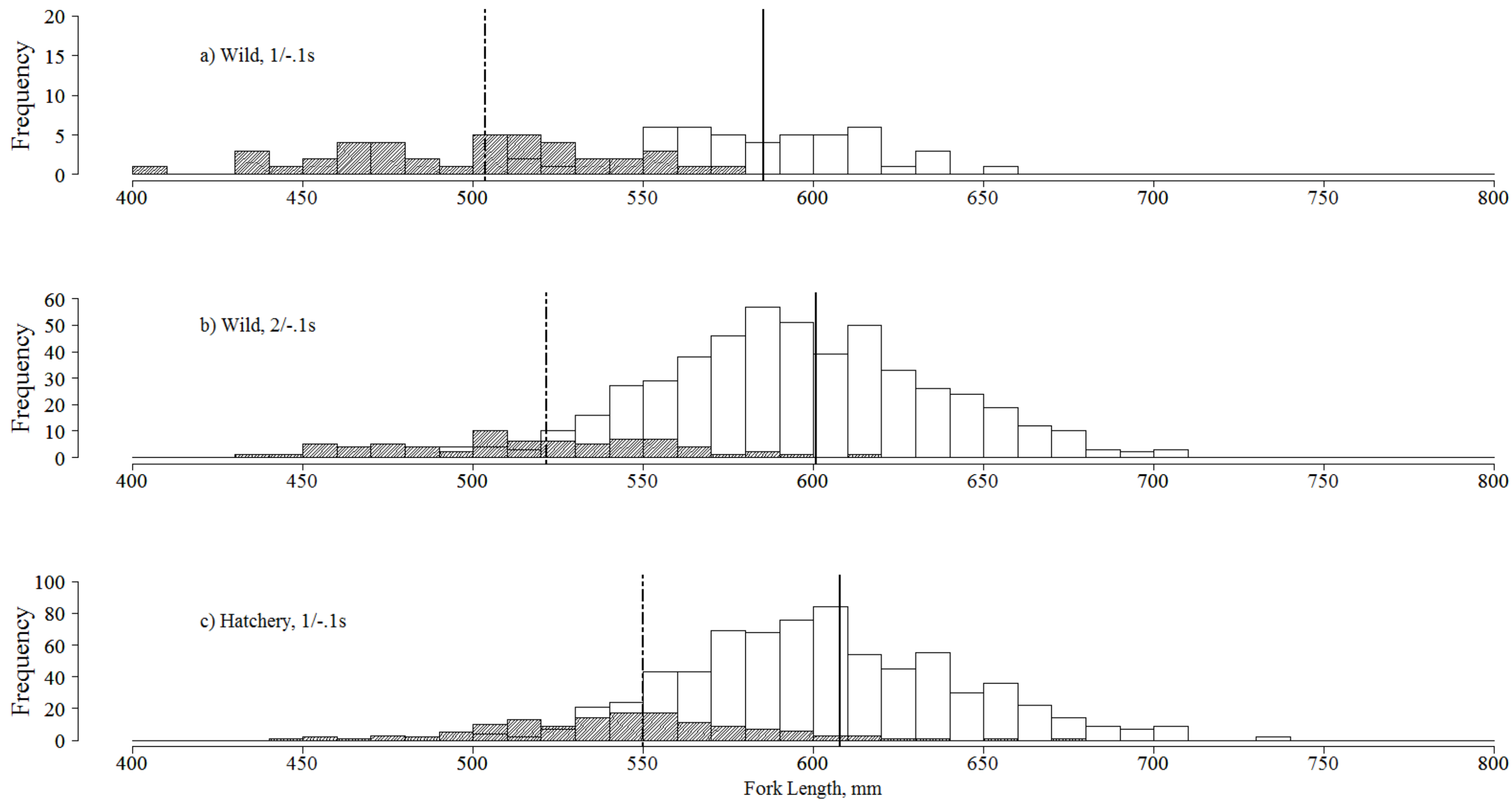

Figure 14. Histograms of fork lengths (mm) of adult wild and hatchery steelhead that did (hatched bars) and did not (open bars) go on half-pounder migration (a/h.1s and a/1.1s, respectively) returning to the Trinity River from 1982 to 2009. Solid vertical line represents mean fork length of steelhead that did not go on half-pounder migration and dashed line represents mean fork length of steelhead that did go on half-pounder migration.

Trinity River Hatchery Smolt Data

Results from change point analysis (Chen and Gupta 1999) indicated that a significant change in mean and variance of size at release apparently occurred after release year 1991 (Figure 15). Mean weight of releases for the period 1979 to 1991 was 55.3 grams, whereas mean weight of releases for the period 1992 to 2007 was 99.4 grams (Figure 15). Estimated variation among release group mean weights was noticeably less for the first period than for the second period. The most likely change point between periods of mean weights is in 1991, which has the lowest Schwarz Information Criterion value (α = 0.05, SIC(k) = 246.30) (Table 12).

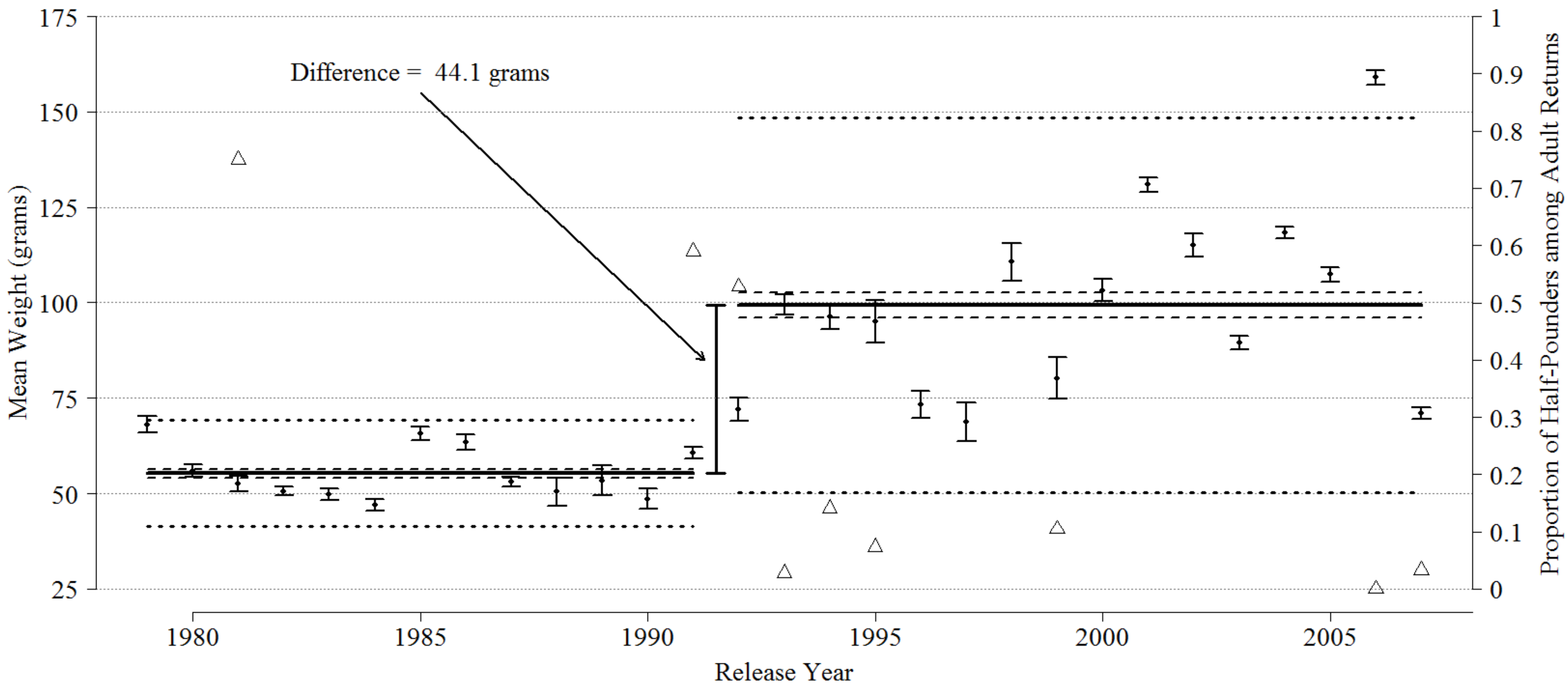

Figure 15. Means (denoted by closed circles, based on weighted averages) and 95% confidence bounds for mean weights of age-1 steelhead smolts released from Trinity River Hatchery from 1979 to 2007. Solid horizontal lines represent period specific means of releases (1979-1991, 1992-2007); dashed horizontal lines represent 95% confidence bounds around the estimated period-specific mean weight at release; and dotted horizontal lines represent 95% confidence intervals around the distribution of means release weights across years within each time period. Open triangles represent estimated half-pounder proportions among returning adults in run year immediately following release.

Table 12. Schwarz Information Criterion (SIC) values used to determine year of change (change point) in mean weights of releases of Trinity River Hatchery steelhead.

Release Year	Estimated Mean Weight (g)	SIC(k)
1979	68.10	NA
1980	55.97	284.89
1981	52.50	282.35
1982	50.61	279.33
1983	49.71	275.90
1984	47.04	*272.46*
1985	65.74	*271.44*
1986	63.36	*268.95*
1987	53.10	*264.83*
1988	50.44	*260.55*
1989	53.41	*255.72*
1990	48.61	*250.61*
1991	60.62	***246.30***
1992	72.00	*247.50*
1993	99.41	*262.01*
1994	96.37	*267.19*
1995	95.06	*270.19*
1996	73.39	*268.28*
1997	68.79	*265.19*
1998	110.64	*271.14*
1999	80.26	*269.64*
2000	103.23	*272.31*
2001	130.90	279.46
2002	115.12	282.32
2003	89.61	281.76
2004	118.32	284.27
2005	107.35	284.86
2006	158.97	NA
2007	71.14	NA

* Italics denote significance at $\alpha = 0.05$ level when compared to SIC(n) and bold denotes most likely change point (i.e. lowest value of SIC(k)).

DISCUSSION

With the exception of several return years in the early 1990s, estimated half-pounder proportions among returning Trinity River adult steelhead have been less than 0.200. These findings are in contrast with reports published by Everest (1973), Hopelain (1998) and contemporary results from the Klamath River basin (Hodge 2010), all of whom reported high half-pounder proportions (though calculated differently) for most of their sample locations and years. However, lower half-pounder proportions were reported from steelhead from the North and South forks of the Trinity River (possibly summer run steelhead) and for winter-run steelhead from the Lower Klamath River (Hopelain 1998) and from the Rogue River (Oregon Department of Fish and Wildlife 1990, Table 7).

Hopelain (1998) estimated the half-pounder proportion among returning Trinity River adult steelhead in 1982 to be 0.80. However, I reexamined the scale samples that Hopelain (1998) used. His estimate is based on a sample size of just 45 adult steelhead and, more importantly, neglected spawning status (maiden or repeat spawners) and the age at which those steelhead entered the ocean. My estimates of half-pounder proportions for wild steelhead that entered the ocean in 1981 after one and two years in freshwater remained high: 1.000 and 0.714, respectively.

Back-calculated fork lengths and age composition at ocean entry of wild steelhead from this study are consistent with results from other studies on the Klamath River basin (Kesner and Barnhart 1972, Hopelain 1998, Hodge 2010). Mean fork lengths of outmigrating smolts (wild and hatchery) from downstream migrant traps operated on the Trinity River (rkm 34) were compared with the back-calculated length at the apparent end of the freshwater zone and were similar. Back-calculated fork lengths at the apparent end of the freshwater zone from wild adult steelhead from this study were also consistent with sizes of similarly aged wild steelhead smolts from within the Klamath River basin (Trinity River and Shasta River). They were also consistent with fork lengths from outside the Klamath River basin (Redwood Creek in northern California, Scott Creek in central California, Columbia River in Washington, and from the Keough River in British Columbia, Canada) (Table 13).

Within a cohort of age *a* smolts, the life history type *a*/1.1s is typically substantially larger than the life history type *a*/h.1s. This finding is consistent with Hopelain (1998), who examined the relationship between half-pounder occurrence and mean fork length at first spawning in 11 different Klamath steelhead stocks. Identifications of half-pounder checks using objective statistical criteria and standard visual classification methods were in very good agreement with one another. Agreement between the two classification methods was good enough that the standard visual classification could be used with confidence on scale samples for which Table 1 measurements were not taken. There were slight differences between estimates of half-pounder proportions derived from both classification methods. Visual classification methods produced 4-20% higher estimates of half-pounder proportions when compared to statistical classification methods (Table 3).

Table 13. Mean sizes of wild and hatchery steelhead smolts documented from seven studies in the Pacific Northwest. Mean fork lengths are reported as yearly means or study-long means.

Origin	Age at Ocean Entry	Mean Fork Lengths (mm)	Mean Type	Location	Source
Wild	2	174, 160, 180, 161, 187, 170	Yearly	Keogh River, British Columbia	Ward et al. 1989 [a]
Wild	2	162, 168	Yearly	Upper Columbia River, Washington	Peven et al. 1994 [a]
Wild	2	165	Study	Upper Redwood Creek	Sparkman 2009 [a]
Wild	2	195	Study	Scott Creek	Bond et al. 2008 [a]
Wild	2	182, 199	Yearly	Shasta River	Chesney 2000 [a]
Wild	2	234	Study	Klamath River	Hodge 2010 [b, c]
Wild	2	224	Study	Salmon River	Hodge 2010 [b, c]
Wild	2	261	Study	Shasta River	Hodge 2010 [b, c]
Wild	2	180, 178, 172, 176, 169, 242, 159, 174	Yearly	Trinity River	U.S. Fish and Wildlife Service 1991 [a], 1994 [a], 1998 [a], 2001 [a]Pinnix et al. 2007 [a], Pinnix and Quinn 2009 [a]
Wild	2	170	Study	Trinity River	My study [b]
Wild	2	148	Study	Trinity River	My study [c]
Hatchery	1	212, 204, 211, 235, 224, 193	Yearly	Trinity River	U.S. Fish and Wildlife Service 1991[a], 1994 [a], 1998 [a], 2001 [a]Pinnix et al. 2007 [a], Pinnix and Quinn 2009 [a]
Hatchery	1	231, 227, 237, 246, 248, 247, 259, 243, 229	Yearly	Trinity River	My study [b]

[a] From observed smolts; [b] From back-calculated fork lengths from adults; [c] From back-calculated fork lengths from half-pounders.

As described in Appendix A, (Figure 16), steelhead life history, especially in combination with the half-pounder life history, is complex. Variable freshwater and marine environments may contribute to interannual variation in estimated half-pounder proportions through their influence on period-specific survival probabilities. For example, high estimated half-pounder proportions may reflect unusually high survival probabilities during the freshwater period of the half-pounder run, $S_{F,w}(t)$, or during the subsequent ocean summer, $S_{O,s}(t+1)$, rather than other factors such as size at ocean entry or at the end of the freshwater zone. Such interannual variation in relative survival rates may limit some of the conclusions that can be drawn from analyses of estimated half-pounder proportions among maiden adult spawners. Despite the strong interannual variation in the estimates of half-pounder proportions, however, both age at ocean entry and size at the end of the freshwater zone appear to be strongly associated with estimated half-pounder proportions, especially among wild Trinity River steelhead. Wild steelhead that entered the ocean as age-1 smolts consistently had higher estimated half-pounder proportions than wild age-2 smolts. Hatchery steelhead that entered the ocean as age-1 smolts almost always had higher estimated half-pounder proportions than wild age-2 smolts. Of all adult steelhead that outmigrated as age-3 smolts (n = 31), only two exhibited a half-pounder check.

Results from logistic regression analyses indicated that the size of wild steelhead at the end of the freshwater zone affected the probability of a subsequent half-pounder run for that particular steelhead. In most models, the back-calculated fork length at the end of the freshwater zone was associated with a negative model coefficient so that larger steelhead at the end of freshwater zone were less likely to return as half-pounders than were smaller steelhead of the same age.

Results from scale analyses suggest that a decline in half-pounder proportions among hatchery steelhead may have occurred over the period 1982 - 2009. The estimated proportion from hatchery adults from 1982 is only based on eight returning adults, however, and the estimated proportion from hatchery adults returning in 1991 should be disregarded due to extremely small sample size (n = 2). Unfortunately, scales were not collected during the mid-1980s to allow examination of a possible trend from 1983 to 1990. Size-at-release of hatchery steelhead smolts (weighted averages of batch releases) has increased and become more variable over the study period. Associated with this increased size is the apparent decrease in estimated half-pounder proportions over approximately the same period.

Many studies have shown that larger size-at-release of salmonids can increase survival during subsequent phases of life (Tipping 1986, Ward and Slaney 1988, Tipping 1997, Bond et al. 2008). In my study, it appears that size-at-age of steelhead may influence the “decision” of a steelhead to go on a half-pounder run or not. Results from logistic regression analyses support this hypothesis. Smaller, slower-growing steelhead in a cohort at time of ocean entry may be more likely to undergo a half-pounder migration than faster growing steelhead of the same cohort.

There are important life history tradeoffs that are a consequence of the half-pounder strategy. First, size (and presumably fecundity) at adult maturity are less for adults of the same age that have not exhibited a half-pounder migration. Second, some energy must be spent transitioning between freshwater and marine environments. Third, there is little opportunity to reproduce as a half-pounder because almost all half-pounders are immature at time of freshwater reentry and during their freshwater residence (Kesner and Barnhart 1972, Hodge 2010). Given these tradeoffs, it seems clear that survival probabilities for half-pounders in freshwater must, on average, exceed survival probabilities for steelhead that remain in the ocean for the winter (see also Satterthwaithe 1988). Otherwise, the half-pounder life history pattern would not persist over an evolutionary timescale.

Management Implications and Further Studies

Since both wild and hatchery steelhead that have undergone a half-pounder migration are smaller than adults from the same cohort that have not, size-selective hatchery mating practices (selecting for matings between the largest males and largest females) might decrease the chance of breeding adult steelhead that have undergone the half-pounder migration. Despite formal guidelines that called for random mating of males and females, hatchery staff at Washington's Forks Creek Hatchery tended to select steelhead with large body size and early run-timing (McLean et al. 2005). Run timing, body size and age at maturity of steelhead trout have all been found to have heritable components (Siitonen and Gall 1989, Mackey et al. 2001). No research to date has investigated the heritability of the half-pounder phenotype or of other phenotypes that may be linked to the unique migration behavior.

For Trinity River steelhead, size at the end of the freshwater zone appears to affect the tendency for an individual steelhead to undergo a half-pounder migration. Change point analysis supports the conclusion that mean size-at-release of hatchery steelhead smolts from Trinity River Hatchery has increased and become more variable since the early 1990s. This increased size may possibly be associated with the low half-pounder proportions that have been observed since 1992. The process of selecting and mating steelhead, as well as rearing and release practices, in hatcheries on the Klamath and Rogue rivers should be examined to ensure that unique phenotypic traits such as the half-pounder life history are maintained over time.

Further research should include using tagged releases, such as passive integrated transponders (PIT tags), of smolts from Trinity River Hatchery. Tagged releases would provide valuable data to estimate survival rates between the different life history types, to investigate the relationship between size at release and life history decisions, to validate scale patterns observed on scales from adults and yield information on residence, and on movement and growth patterns of the alternate life history patterns. Simulation models might be used to evaluate freshwater or marine conditions in which the half-pounder migration may be costly or beneficial at a population level. Finally, continued scale sample collections from wild and hatchery adults from the Willow Creek weir using standardized protocols should be implemented to monitor both half-pounder proportions and frequency of repeat spawning.

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APPENDIX A

The developed life history model (introduced in Methods) was used to provide insight about the complexity of both steelhead life history and the development of an unbiased estimate or index of the tendency of a steelhead to return as a half-pounder. The various life history pathways of Trinity River steelhead are shown in Appendix Figure A.1. The model assumes that steelhead were the fall-run ecotype as described previously. Let $N_a(t)$ equal the number of smolts that enter the ocean at age a (a = 1,2,3) in March through May of year (t). Let $S_{O,s}(t)$ denote survival rates during the first ocean summer after ocean entry; $S_{O,w}(t)$ denote survival rates of the first ocean winter for steelhead that remain in ocean; $S_{F,w}(t)$ denote survival rates of the first freshwater winter for steelhead on the half-pounder migration. Analogous notation is used to represent survival rates of steelhead in the ocean or in freshwater in successive years (t+1 and t+2).

Conditional maturation probabilities given smolt age and previous life history are designated using notation consistent with Hopelain's (1998) designations of life histories. For example, $\sigma_{a|h.1s}$ is the probability that a steelhead will mature on its first possible adult spawning run given it is an age a smolt that had returned previously as a half-pounder.

$\sigma_{a|h}$ = P(mature as half-pounder given age a smolt and alive at 15 August in year t)

$\sigma_{a|h.1s}$ = P(mature on first possible adult spawning run given age a smolt that had returned as half-pounder)

$\sigma_{a|1.1s}$ = P(mature on first possible adult spawning return given age a smolt that did not return as half-pounder)

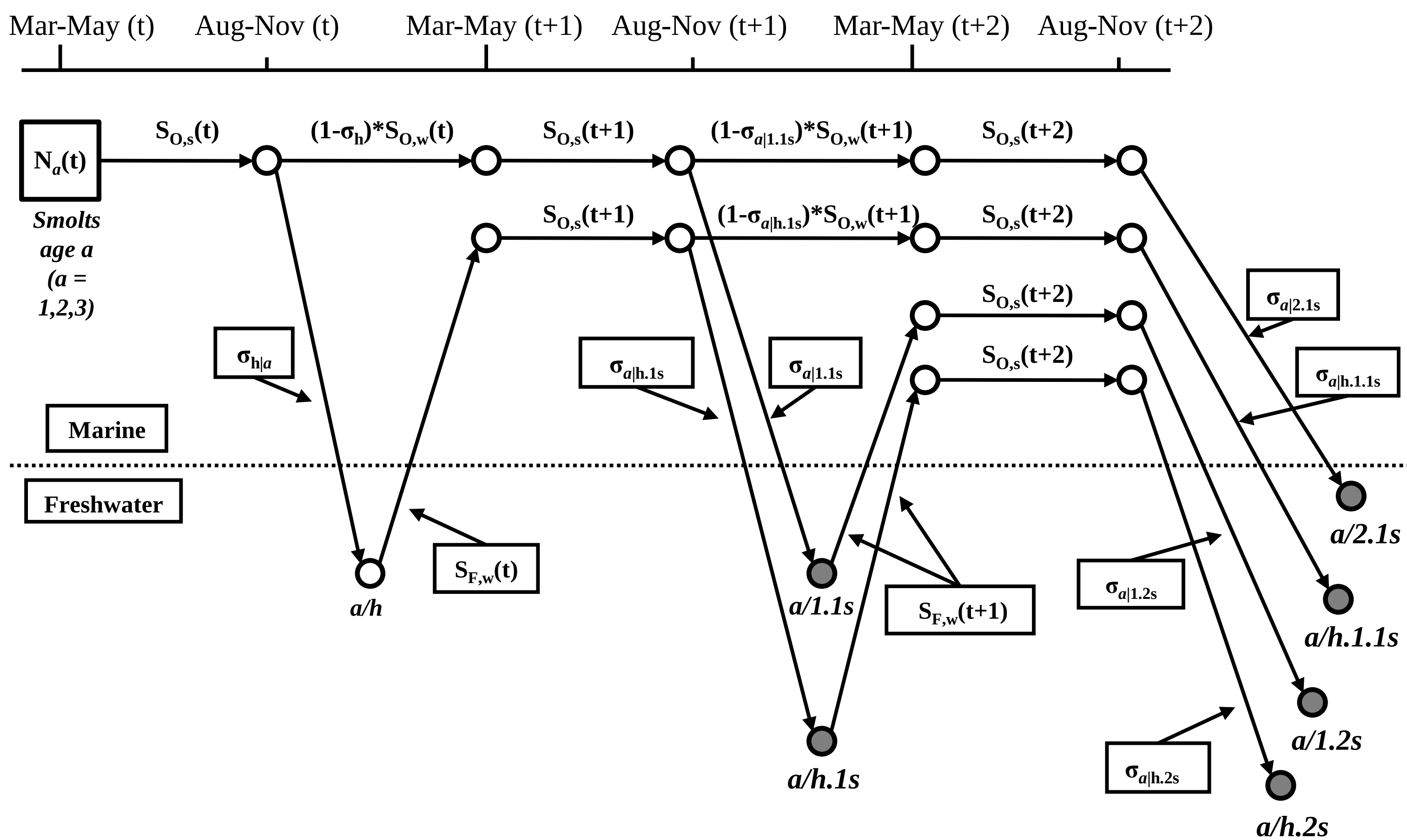

Figure 16. Diagrammatic representation of potential life histories of Trinity River steelhead after ocean entry and corresponding adult age designations. Unfilled circles represent nodes at which steelhead may choose different life history pathways and filled circles represent mature adult steelhead on spawning runs. Dates are given to represent the general outmigration or return periods. Notation is explained in the text.

$\sigma_{a|1.2s}$ = P(mature on second possible adult spawning run given age *a* smolt that did not return as a half-pounder and returned as adult on first possible adult spawning run)

$\sigma_{a|h.1.1s}$ = P(mature on second possible adult spawning run given age *a* smolt that had returned as half-pounder and did not previously returned as an adult)

$\sigma_{a|2.1s}$ = P(mature on second possible adult spawning run given age *a* smolt that did not return as half-pounder and did not return on first possible adult spawning run)

$\sigma_{a|h.2s}$ = P(mature on second possible adult spawning run given age *a* smolt that had returned as half-pounder and returned as adult on first possible adult spawning run)

For any particular life history group, the expected number of steelhead that would exhibit that life history type can be calculated as the product of the initial number of smolts ($N_a(t)$) and all subsequent parameters (survival rates and conditional maturation probabilities) leading to that specific life history pathway (Figure 16). For example, the expected number of steelhead in life history group, *a*/1.1s, can be calculated as:

$$E(N_{a/1.1s}) = N_a(t)\ S_{O,s}(t)\ (1-\sigma_{a|h})S_{O,w}(t)\ S_{O,s}(t+1)\sigma_{a|1.1s}$$

The following list provides expected numbers for each life history group, given $N_a(t)$:

$$E(N_{a/h.1s}) = N_a(t)\ S_{O,s}(t)\ \sigma_{a|h}\ S_{F,w}(t)\ S_{O,s}(t+1)\ \sigma_{a|h.1s}$$

$$E(N_{a/1.1s}) = N_a(t)\ S_{O,s}(t)\ (1-\sigma_{a|h})S_{O,w}(t)\ S_{O,s}(t+1)\sigma_{a|1.1s}$$

$$E(N_{a/h.2s}) = N_a(t)\ S_{O,s}(t)\ \sigma_{a|h}\ S_{F,w}(t)\ S_{O,s}(t+1)\ \sigma_{a|h.1s}\ S_{F,w}(t+1)\ S_{O,s}(t+2)\ \sigma_{a|h.2s}$$

$$E(N_{a/1.2s}) = N_a(t)\, S_{O,s}(t)\, (1-\sigma_{a|h}) S_{O,w}(t)\, S_{O,s}(t+1)\, \sigma_{a|1.1s} S_{F,w}(t+1)\, S_{O,s}(t+2)\, \sigma_{a|1.2s}$$

$$E(N_{a/h.1.1s}) = N_a(t)\, S_{O,s}(t)\, \sigma_{a|h}\, S_{F,w}(t)\, S_{O,s}(t+1)(1- \sigma_{a|h.1s})\, S_{O,w}(t+1)\, S_{O,s}(t+2)\, \sigma_{a|h.1.1s}$$

$$E(N_{a/2.1s}) = N_a(t)\, S_{O,s}(t)\, (1-\sigma_{a|h}) S_{O,w}(t)\, S_{O,s}(t+1)(1- \sigma_{a|1.1s})\, S_{O,w}(t+1)\, S_{O,s}(t+2)\, \sigma_{a|2.1s}$$

As described in the Methods section, half-pounder proportions were estimated by determining the fraction ($\hat{\rho}$) of steelhead that exhibited the half-pounder check from scales of steelhead on their first possible adult spawning run. The expected value of $\hat{\rho}$, however, is not in general equal to $\sigma_{a|h}$, the probability of maturing as a half-pounder given smolt age a. Instead, assuming that all first spawning adults are equally vulnerable to collection at some rate α (whether or not they first matured as a half-pounder) this calculation should give, in expectation:

$$E(\hat{\rho}) \approx \frac{E(n_a/h.1s)}{E(n_a/h.1s) + E(n_a/1.1s)}$$

$$= \frac{\alpha E(N_a/h.1s)}{\alpha E(N_a/h.1s) + \alpha E(N_a/1.1s)}$$

$$= \frac{N_a(t)\, S_{O,s}(t)\, \sigma_{a|h}\, S_{F,w}(t)\, S_{O,s}(t+1)\sigma_{a|h.1s}}{N_a(t) S_{O,s}(t)\left(1 - \sigma_{a|h}\right) S_{O,w}(t) S_{O,s}(t+1)\sigma_{a|1.1s} + N_a(t)\, S_{O,s}(t)\, \sigma_{a|h}\, S_{F,w}(t)\, S_{O,s}(t+1)\sigma_{a|h.1s}}$$

$$= \frac{\sigma_{a|h}\, S_{F,w}(t)\sigma_{a|h.1s}}{\left(1 - \sigma_{a|h}\right) S_{O,w}(t)\sigma_{a|1.1s} + \sigma_{a|h}\, S_{F,w}(t)\, \sigma_{a|h.1s}}.$$

Obviously, this calculation is not algebraically equivalent to the target of estimation, $\sigma_{a|h}$. If, however, it were reasonable to suppose that $S_{F,w}(t) = S_{O,w}(t) = S$ and $\sigma_{a|h.1s} = \sigma_{a|1.1s} = \sigma$, then:

$$E(\hat{\rho}) = \frac{\sigma_{a|h}\, S\, \sigma}{\left(1 - \sigma_{a|h}\right) S\, \sigma + \sigma_{a|h}\, S\, \sigma} = \frac{\sigma_{a|h}\, S\, \sigma}{S\, \sigma} = \sigma_{a|h}.$$

Based on the small number of steelhead that first mature after two full ocean years (i.e., there are very few steelhead of life history types a/h.1.1s or a/2.1s), it is reasonable to assume that $\sigma_{a|h.1s} \cong \sigma_{a|1.1s}$ and that both are probably close to one. Many lines of reasoning (see Discussion), however, support the assumption that $S_{F,w}(t)$ must, on average, be greater than $S_{0,w}(t)$. If $\sigma_{a|h.1s} = \sigma_{a|1.1s} = 1$, then:

$$E(\hat{\rho}) \approx \frac{\sigma_{a|h}\ S_{F,w}(t)}{(1-\ \sigma_{a|h})S_{0,w}(t) +\ \sigma_{a|h}\ S_{F,w}(t)}. \tag{8}$$

The numerator of equation (8) will be less than $S_{F,w}(t)$ whenever $S_{F,w}(t) > S_{0,w}(t)$. Therefore, estimates of half-pounder proportions from scale analysis using equation (3) will generally be positively biased and will overestimate the true tendency of steelhead to mature as half-pounders, $\sigma_{a|h}$. The degree of positive bias should be small, however, unless $S_{F,w}(t)$ greatly exceeds $S_{0,w}(t)$.

APPENDIX B

Because Trinity River Hatchery reports did not include estimates of error for size at release, I relied on unpublished length and weight data of juvenile Trinity River Hatchery steelhead from Naman (2008) to develop 95% confidence intervals around the weighted means. Naman (2008) captured (with dipnets) and weighed (±0.1g) fifty juvenile hatchery steelhead from each of ten raceways at the Trinity River Hatchery 14 March 2007, one day prior to release. For each raceway, an estimate of coefficient of variation ($\widehat{CV}$) was calculated using:

$$\widehat{CV}_h = \frac{\hat{\sigma}_h}{\hat{\mu}_h}, \tag{9}$$

where $\hat{\sigma}_h$ = estimated standard deviation of mean weight; and $\hat{\mu}_h$ = estimated mean weight of steelhead from raceway h. A strong inverse linear relationship was found between $\hat{\mu}_h$ and $\widehat{CV}_h$ (adjusted $R^2 = 0.8417$).

From this linear relationship ($\widehat{CV}_h = 0.6355 - 0.0040\, \hat{\mu}_h$), an estimated variance of the mean weight was calculated for each raceway using:

$$\hat{\sigma}_h^2 = (\widehat{CV}_h \hat{\mu}_h)^2. \tag{10}$$

Prior to release, hatchery personnel at Trinity River Hatchery draw three 5 lb samples of yearling steelhead from each raceway (one sample each from the front, middle, and back of each raceway) and the numbers of fish in each of these samples are averaged to generate the reported size at release, expressed as numbers of fish/lb (Zajanc and Hankin 1998). Under a stratified random sampling design with L strata (raceways), the variance of the estimated overall mean in year i, $\hat{V}(\hat{\mu}_i)$, can be calculated using:

$$\hat{V}(\hat{\mu}_i) = \sum_{h=1}^{L} W_h^2 \, \hat{V}(\hat{\mu}_h), \tag{11}$$

where:

$$W_h = \frac{N_h}{N} = \frac{N_h}{\sum_{h=1}^{L} N_h}; \tag{12}$$

and;

$$\hat{V}(\hat{\mu}_h) = \frac{\hat{\sigma}_h^2}{n_h}, \tag{13}$$

where: n_h = number of steelhead sampled from each strata, calculated by multiplying the reported average number of fish per pound in a release group by 15 lbs (the total weight of the three 5 lb samples). Confidence intervals (Thompson 2002) were then constructed around the estimated weighted mean in release year using:

$$\hat{\mu}_i = 2\sqrt{\hat{V}(\hat{\mu}_i)}. \tag{14}$$

To aid interpretation of the results of change point analysis (see Statistical Analyses) of hatchery steelhead release weights, I wished to construct 95% confidence bounds around the estimated means for two identified periods and to characterize the variation in mean release weights across years within each of two periods. For each period, I estimated overall unweighted mean size at release using:

$$\bar{\hat{\mu}}_j = \frac{1}{k} \sum \hat{\mu}_i, \tag{15}$$

where k = number of years in period j. I constructed approximate 95% confidence bounds around this estimate as: $\bar{\hat{\mu}}_j \pm 2\sqrt{\frac{1}{k^2} \sum_{i=1}^{k} \hat{V}(\hat{\mu}_i)}$, (16) Additionally, for each period, approximate 95% confidence bounds were constructed around the actual mean weight at release in any particular year within period j using:

$$\bar{\hat{\mu}}_j \pm 2\sqrt{\frac{1}{k}\sum_{i=1}^{k}\frac{(\hat{\mu}_i - \hat{\bar{\mu}})^2}{k-1}}. \tag{17}$$

Methods used to construct the above approximate confidence bounds are motivated by fundamental results in two-stage sampling (e.g., Jessen 1978, equation 9.24) and by the important distinction between prediction of the expected value of a random variable as opposed to the particular value that the variable may take on, as illustrated in linear regression (e.g., Zar 1984, Equations 17.26 vs. 17.29).