LIFE HISTORY VARIATION IN ONCORHYNCHUS MYKISS FROM THE LOWER KLAMATH RIVER BASIN

By

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ABSTRACT

Life History Variation in *Oncorhynchus mykiss* from the Lower Klamath River Basin

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The lower Klamath River Basin supports the most productive steelhead (*Oncorhynchus mykiss*) fishery in the state of California, and is one of only several fisheries in the world in which steelhead exhibit the unique half-pounder life history. Half-pounders exhibit a largely amphidromous (i.e., non-reproductive) migration in which individuals return to the river several months after initial ocean entry, overwinter in freshwater, and return to the ocean the following spring. Current information on the incidence and attributes of the half-pounder and other life history forms in the lower Klamath River is not available. Objectives of this study were i) to describe patterns of age and growth, as well as migratory and reproductive history in wild *O. mykiss* from the lower Klamath River Basin, ii) to evaluate the influencing factors (i.e., size and natal origin) in expression of life history, and iii) to explore the growth and fecundity consequences of differing life history patterns. From August 2007 through April 2009, otoliths, scales, and biological data (i.e., length, weight, and sex) were collected from fish that were captured with hook and line and at weir trapping facilities. To determine migratory history (anadromous versus nonanadromous) and maternal origin (anadromous versus nonanadromous) of *O. mykiss*, I analyzed otolith strontium isotope ratios ($^{87}Sr/^{86}Sr$). To determine age, growth, and life history, I performed qualitative scale analysis. Half-pounders were examined to determine sex and incidence of reproductive maturity, and biological data were collected from adult, female steelhead to quantify the relationship between length and fecundity. Otolith microchemistry indicated that anadromous and nonanadromous forms of *O. mykiss* occur sympatrically in the lower Klamath River Basin. Further, otolith microchemistry suggested that steelhead and rainbow trout may give rise to progeny of the alternative life history form. Including anadromous and nonanadromous forms, *O. mykiss* from the basin exhibit at least 33 different life history categories at maturity; which differ in the number of years of freshwater and saltwater residency, expression of a half-pounder migration, and number of spawning runs. Among sub-basins, incidence of resident rainbow trout ranged from 1.2% in the Trinity River to 57.2% in the Scott River, and incidence of the half-pounder life history ranged from 11.0% in the Trinity River to 100.0% in the Shasta River. Approximately 7.6% of half-pounders attained full maturity after spending less than one year at sea. Adult steelhead that exhibited the half-pounder life history were smaller and less fecund at age than fish that remained in the ocean; however results of life history analysis suggest that continued expression of the half-pounder phenotype is favored by precious maturation and enhanced survival relative to the ocean contingent phenotype. My finding regarding the ability of rainbow trout to give rise to steelhead has important management implications in the Klamath River Basin, where the scheduled removal of four dams is expected to restore connectivity between the ocean and the upper basin. Following dam removal, resident *O. mykiss* in the upper basin may be able to contribute towards recovery of the steelhead population.

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INTRODUCTION

Oncorhynchus mykiss exhibit a great deal of variation in life history and reproductive biology (Shapovalov and Taft 1954; Barnhart 1986; Busby et al. 1996). For example, *O. mykiss* exhibit partial migration: fish exist in both anadromous (steelhead) and nonanadromous (resident rainbow trout) forms (Behnke 1992; Jonsson and Jonsson 1993; Busby et al. 1996). These alternative life history forms may occur sympatrically; in limited (Seamons et al. 2004; McPhee et al. 2007; Pearsons et al. 2007), partial (Docker and Heath 2003; Narum et al. 2004), or total genetic isolation (Zimmerman and Reeves 2000).

Including anadromous and non-anadromous forms, *O. mykiss* may follow one of 32 different maturation trajectories (Thorpe 1998, 2007). Rainbow trout reside in freshwater for the duration of their lives, and reach maturity in 1-5 years. While rainbow trout never migrate to sea, residents may migrate within rivers or between nearby lakes and streams (Meehan and Bjornn 1997; Moyle 2002; Narum et al. 2004; Quinn 2005). Steelhead spend 1-7 years in freshwater, and from several months to four years in the ocean before returning to spawn (Busby et al. 1996). Most, if not all, of the fish that return to spawn after spending less than one year at sea are male ("jacks"; Willson 1997; Moyle 2002; Quinn and Meyers 2004). Regardless of sea age, all steelhead belong to one of two basic reproductive ecotypes that differ in both the season and state of maturity upon freshwater re-entry. Summer (stream-maturing) steelhead enter freshwater between May and October in a state of immaturity, whereas winter (ocean-maturing) steelhead enter freshwater between November and April in an advanced state of maturity. Runs within these two ecotypes often acquire names (e.g., spring and fall) based upon the peak timing of migration (Busby et al. 1994; Busby et al. 1996).

Both resident and anadromous forms of *O. mykiss* are facultatively iteroparous, though repeat spawning is more prevalent in residents than in sea-run fish (Fleming 1998; Quinn 2005). While steelhead are capable of spawning up to five times, most fish are maiden spawners, and very few survive beyond two spawning migrations. Incidence of iteroparity is greater in female steelhead than in male steelhead (Busby et al. 1996; Willson 1997; Moyle 2002).

The Klamath River Basin below Iron Gate Dam, hereafter referred to as the lower basin, supports a population of *O. mykiss* in which the phenotypic plasticity of the species is well illustrated. Previous studies indicate that most fish are anadromous (Kesner and Barnhart 1972; Hopelain 1998), though resident trout have been observed in both wild (Quinones, unpublished data) and hatchery stocks (Chesney 2003; Donohoe et al. 2008; Naman 2008). In addition to the typical variation of steelhead pathways, fish in the lower Klamath River Basin also exhibit the “half-pounder” life history (Snyder 1925; Kesner and Barnhart 1972; Hopelain 1998). Half-pounders are steelhead that return to the river several months after initial ocean entry, overwinter in freshwater, and return to the ocean the following spring (Kesner and Barnhart 1972; Everest 1973; Hopelain 1998). Incidence of the half-pounder life history is apparently more prevalent in summer steelhead than in the winter steelhead (McPherson and Cramer 1982; Hopelain 1998). In contrast to the typical adult steelhead, half-pounders feed extensively in freshwater, and rarely spawn during this overwintering period (Kesner and Barnhart 1972; Everest 1973; Savvaitova 2005). For years this seemingly "amphidromous" (McDowall 1997) migration was considered unique to steelhead in the Klamath, Eel, Mad, and Rogue Rivers of Northern California and Southern Oregon (Snyder 1925; Kesner and Barnhart1972; Everest 1973; Busby et al. 1996; Hopelain 1998); however, a similar life history has been observed recently in stocks from Russia (Savvaitova et al. 2005), and in North American stocks transplanted to Argentina (Pascual et al. 2001).

Although the lower Klamath River Basin supports the largest and most popular steelhead fishery in California (CDFG 1998; Hopelain 1998), relatively little is known about current *O. mykiss* life history patterns. To date, only a single publication has addressed among stock variation in life history patterns on a basin-wide scale, and the results of that study came from data collected during 1980-1983 (Hopelain 1998). Subsequently, a population decline led to the closure of the wild steelhead fishery in 1997. Natural or anthropogenic change can alter life history pathways, and fishery managers would benefit from an enhanced ability to anticipate life history responses to variations in environment and resource policy (Satterthwaite et al. 2009). This predictive capability will only come through a comprehensive understanding of how biological and physical factors influence the expression of life history traits (Marschall et al. 1998; Moyle et al. 2008). Because 86-100% of fall-run steelhead stocks in the lower Klamath River Basin exhibit the half-pounder life history, it appears especially important to identify both the factors affecting the expression of the life history and the consequences of this trajectory.

To date, no consensus exists as to what ecological conditions promote the half-pounder life history (Quinn 2005), nor does a consensus exist as to what selective pressures favor the continued expression of the life history (Busby et al. 1994; Busby et al. 1996). Also unknown is the role of genetic and environmental cues influencing the expression of the trait (Busby et al. 1994). Several hypotheses to account for the existence of the half-pounder life history have emerged, though each lacks substantiation. For example, Snyder (1925) suggested that half-pounders are maiden spawners. However, subsequent studies indicated that only a small proportion (3.6-9.6%) of half-pounders will spawn in winter, the majority of which will be male (Kesner and Barnhart 1972; Everest 1973; Savvaitova 2005). Satterthwaite (1988) proposed that selection favors the life history because half-pounders are likely to experience greater winter survival in freshwater than “ocean contingents” experience at sea. Supporting evidence is sparse and anecdotal. Savvaitova et al. (2005) suggested that half-pounders spend the summer in brackish water and winter in freshwater to complete an osmo-regulatory transformation necessary to enter full seawater, however this does not explain why fish adapted to estuary or coastal areas would return to freshwater before proceeding to the high seas.

In accordance with the expectations of life history theory (e.g., Gross 1987; Hendry et al. 2004), the half-pounder life history should only persist if on average, the positive fitness consequences (benefits) of entering freshwater equal or outweigh the negative fitness consequences (costs). Further, incidence of the life history should vary among populations in response to changes in the relative benefits and costs of the migration. Because there is strong negative relationship between length at first-time spawning and incidence of the half-pounder life history (McPherson and Cramer 1982; Hopelain 1998), and typically a positive relationship between size and reproductive success in salmonids (Hendry et al. 2004; Quinn 2005), it appears that there is a significant breeding cost associated with the migration. However, evidence to date is insufficient to determine if fish exhibiting the half-pounder trait exhibit either compensatory growth or greater iteroparity later in life.

Previous studies of steelhead in the lower Klamath River Basin (e.g., Kesner and Barnhart 1972, Collins and Wilson 1994; Hopelain 1998) have relied primarily upon visual examination of scales to identify age, growth, and life history. While scales can be collected in a non-lethal manner and are easily prepared for examination (Lux 1971; Davis and Light 1985; Devries and Fries 1996), visual interpretation of scale patterns is a subjective process (Mann and Steinmetz 1985; Zimmerman et al. 2003). For example, the basis for identifying environmental and migratory history is that freshwater growth is identified by narrow, tightly spaced circuli; and ocean growth is identified by thick, widely spaced circuli (Davis and Light 1985).

Like scales, otoliths (fish ear stones) are also used to reconstruct life history in fishes, and these hard structures offer additional analytical applications. Because the chemical composition of an otolith is primarily a reflection of the water a fish inhabits (Kennedy et al. 2000, Kennedy et al. 2002; Bacon et al 2004; Walther and Thorrold 2008), isotope analysis can serve as an objective method for recreating environmental history. To date, analysis of otolith strontium isotope ratios ($^{87}Sr/^{86}Sr$) has been useful in retrospective determination of natal habitat (Ingram and Weber 1999; Hobbs et al. 2005; Barnett-Johnson and Pearson 2008; Walther and Thorrold 2008), maternal run time (Miller and Kent 2009), intra-basin movement (Kennedy et al. 2000), and anadromous migratory history (Kennedy 2002; Outridge et al. 2002; Bacon et al. 2004; Woodhead et al. 2005). Strontium isotope ratios in fish otoliths serve as an ideal chronological record of environmental history for a number of reasons. First, the $^{87}Sr/^{86}Sr$ ratio of a stream is controlled by the underlying geochemical composition of the distinct watershed, and remains essentially constant through time (Kennedy et al. 2000; Bacon et al. 2004). Second, the $^{87}Sr/^{86}Sr$ ratio of the marine environment is globally uniform (= 0.70918; Kennedy et al. 2000; Bacon et al. 2004; Miller and Kent 2009), and has remained stable for an estimated 400,000 years (Gillanders 2005). Last, otolith $^{87}Sr/^{86}Sr$ ratios are not affected by biological or exterior environmental factors (Kennedy et al. 1997; Kennedy et al. 2000; Kennedy et al. 2002; Outridge et al. 2002).

An additional application of otolith strontium isotope analysis might include determining if *O. mykiss* are progeny of anadromous or non-anadromous maternal origin. Previously, maternal origin has been identified by comparing Sr/Ca ratios in the otolith core (i.e., the region surrounding the primordia) to Sr/Ca ratios in the freshwater growth region (Zimmerman and Reeves 2000; Volk et al 2000; Donohoe et al. 2008; Zimmerman et al. 2009). The utility of this approach is based on the assumption that the chemical composition of the otolith core is a reflection of the environment in which the yolk precursors develop. For steelhead, yolk development presumably begins in the ocean (Kalish 1990). Because $^{87}Sr/^{86}Sr$ ratios in the otolith core are elevated by a marine influence in progeny of anadromous maternal origin (Bacon et al. 2004; Miller and Kent 2009), analysis of strontium isotope ratios should be useful for making the same determination. However, for this to hold true, the geochemical signature of the watershed must be sufficiently different from that of the ocean. Given that the $^{87}Sr/^{86}Sr$ ratio of sea water is significantly higher than any known in-stream ratio in the lower Klamath River Basin (Quinones et al., unpublished), and assuming yolk formation was nearly complete at sea (Kalish 1990; Volk et al. 2000; Zimmerman and Reeves 2002; Zimmerman et al. 2009), progeny of Klamath Basin steelhead should have core $^{87}Sr/^{86}Sr$ ratios that are elevated above ambient stream values.

Objectives of this study were i) to describe patterns of age and growth, as well as migratory and reproductive history in wild *O. mykiss* from the lower Klamath River Basin, ii) to evaluate the influencing factors (i.e., size and natal origin) in expression of life history, and iii) to explore the growth and fecundity consequences of differing life history patterns. To meet the objectives of this study, data were collected in a series of steps. First, scales, otoliths, and biological data (i.e., length, weight, and sex) were collected from *O. mykiss* captured throughout the anadromous waters of the lower

Klamath River Basin. Otolith microchemistry was used to both determine life history form (anadromous versus nonanadromous), migratory history (i.e., movement between freshwater and marine environments), and maternal origin of *O. mykiss* (anadromous versus nonanadromous); and to enable assessment of the accuracy of qualitative scale analysis. Scales were visually examined to determine the age, growth, and life history of fish around the basin. Half-pounders were examined to determine the incidence of maturity, and a model was developed to estimate maturation probabilities. In addition, fecundity data was collected from sexually mature females to quantify the relationship between length and egg number in steelhead from the basin.

MATERIALS AND METHODS

Study Area

The Klamath River drains 40,632 km² of southern Oregon and northern California before emptying into the Pacific Ocean approximately 35 km south of the California-Oregon border (Figure 1). At one time, the Klamath River was the third-largest salmon producer on the West Coast; however, only a fraction of the historic habitat is still accessible to anadromous fishes. Fish migrations are blocked 306 river km (rkm) upstream of the mouth by Iron Gate Dam, which effectively divides the upper and lower basins of the Klamath River. Below the dam, the Klamath is fed by numerous small tributaries and four major tributaries: the Trinity (5,274 km²), Salmon (1,943 km²), Scott (2,107 km²), and Shasta (2,058 km²) Rivers. Anadromous migrations are blocked in the Trinity and Shasta Rivers by Lewiston and Dwinnell dams, which are located 180 rkm and 65 rkm upstream of the confluence with the Klamath, respectively. In addition to *O. mykiss*, the lower Klamath River Basin also supports populations of other anadromous fishes, including: spring and fall-run Chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), cutthroat trout (*O. clarki*), green sturgeon (*Acipenser medirostris*), Pacific lamprey (*Lampetra tridentata*), Pacific eulachon (*Thaleichthys pacificus*), and threespine stickleback (*Gasterosteus aculeatus*). This study focused on the anadromous waters of the lower Klamath River Basin.

Fish Capture and Data Collection

From August 2007 through April 2009, scales and biological data were collected

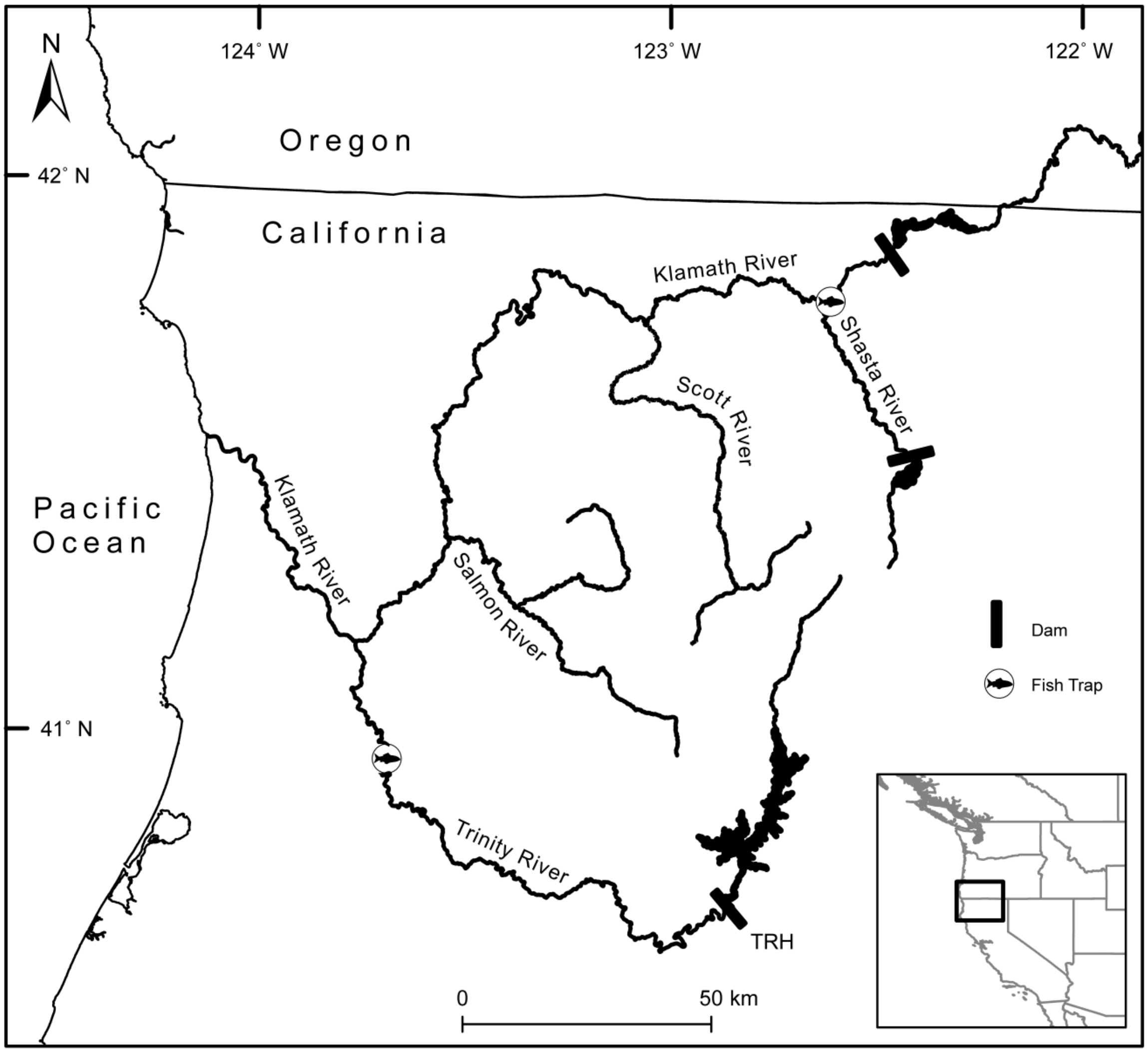

Figure 1. Location of the lower Klamath River Basin in northern California (inset) and a map of the study area (anadromous waters); including locations of fish traps, barriers to anadromy (i.e., dams), and Trinity River Hatchery (TRH).

from wild *O. mykiss* that were captured with hook and line and at weir trapping facilities operated by the California Department of Fish and Game (CDFG). Hook and line sampling was conducted from late summer through early spring (August-April), and collection efforts were focused on anadromous reaches where CDFG traps were absent. *O. mykiss* were trapped and randomly sub-sampled at the Willow Creek Weir on the Trinity River (rkm 35) during August-November in 2007 and 2008, and fish were trapped and sampled on the Shasta River (rkm 1) during October- December 2008 (See Figure1). Sampling dates were selected to coincide with the migration of fall and winter-run steelhead.

After fish were confirmed to be of wild origin by the absence of clipped fins or maxillaries, they were measured (fork length (FL)) to the nearest mm; and sex, date, and location of capture noted. Fork lengths of fish measured at trapping stations by CDFG personnel were measured to the nearest cm. Male fish were identified by a pointed snout and maxillary that extended past the posterior margin of the eye, and female fish were identified by a rounded snout and relatively short maxillary. Scales were removed from the left side of fish at a point located directly below the posterior insertion of the dorsal fin and several rows above the lateral line. Removed scales were placed in waterproof coin envelopes and air-dried. Because of large numbers of half-pounder returns during the fall and winter migration in 2008-2009, scales were removed from a sub-sample of fish presumed to be half-pounders (250-420 mm FL). Because a gap existed between the pickets (metal conduit) of the CDFG weirs, traps were primarily effective in capturing fish greater than 350 mm FL (Sinnen 2009, personal communication).

Validation of Scale Analysis

To improve scale reader performance, and to assess the accuracy of the methods employed, a set of paired otoliths and scales was used for training and validation purposes. First, I analyzed otolith strontium isotope ratios to determine migratory history (anadromous versus nonanadromous, episodes of movement between freshwater and saltwater), and maternal origin (anadromous versus nonanadromous) of a sub-sample of *O. mykiss*. Because this was a calibrated and objective procedure, I assumed that results of otolith microchemistry were 100% accurate in distinguishing between anadromous and nonanadromous fish. Therefore, results were treated as the true, a priori classifications. Next, scales from the same sub-sample of fish were visually analyzed, and the resulting determinations of migratory history were compared to those determinations from otolith microchemistry. Last, to explore how much classification error might be due to errant reader perception versus false assumptions in pattern recognition, the same scale set was analyzed using methods of quantitative scale pattern analysis.

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Otolith Preparation and Microchemical Analysis

Otoliths were collected from a sub-sample of half-pounders and adult steelhead that were originally sacrificed for other purposes (see “Half-Pounder Maturity” and “Fecundity” below; IACUC Protocol # 06/07 F 175A). Sagittal otoliths were extracted with clean forceps, rinsed, and dried. Left sagittae were mounted to glass slides with Crystalbond ™ thermoplastic resin. Right otoliths were used in the event that the left was damaged or showed signs of vaterite: a crystalline form of calcium carbonate.

Otoliths were sectioned around the core along the dorso-ventral axis. Core sections were re-mounted to slides, ground with 1200-grit sandpaper, and polished with a 0.05 µm alumina paste. Sections were flipped and the process repeated. Otolith sections were then washed in 1% nitric acid for 5 to 10 s, rinsed in an ultrasonic bath for 5 minutes, and dried under a class 100 laminar flow hood.

Otolith strontium isotope ratios ($^{87}Sr/^{86}Sr$) were analyzed by laser ablation (LA; Nd: YAG 213-nm laser, New Wave Research UP213) inductively coupled plasma mass spectrometry (ICP-MS; Agilent Technologies 7200A) at the University of California at Davis Interdisciplinary Center for Plasma Mass Spectrometry. Prior to each analytic session, the $^{87}Sr/^{86}Sr$ ratio of an in-house marine carbonate standard was measured by LA-ICP-MS. The average $^{87}Sr/^{86}Sr$ ratio measured was 0.709201 ± 0.000078 (2SE); consistent with previously reported global values of marine carbonate (Outridge et al. 2002; Miller and Kent 2009). Core-to-edge laser transects were ablated at a rate of 10 $\mu m \cdot s^{-1}$ by a 40 µm (diameter) beam, pulsing at a rate of 20Hz. Edge-to-edge transects were analyzed in a sub-sample of otoliths. Ablated material was carried from the laser sample cell by a stream of helium (He) gas, and mixed with argon (Ar) gas before aerosols were sent to the plasma source. Between samples, background and gas blank signals were monitored until ^{84}Kr and ^{86}Kr were stable, and the laser was then turned on for 30-60 s. Measured signals were automatically corrected for background interference, and mass bias was corrected using the $^{86}Sr/^{88}Sr$ ratio of 0.1194. Peak intensities of ^{84}Sr, ^{86}Sr, ^{87}Sr, ^{88}Sr, and ^{85}Rb were measured simultaneously, and intensity of ^{85}Rb was used to correct for interference of ^{87}Rb on ^{87}Sr. Before data were analyzed, visual (digital photographs) and chemical (^{87}Sr/^{86}Sr) cues were used to verify the location of key regions in the otolith (Miller and Kent 2009); including the core, freshwater growth region, and saltwater growth region (Figure 2).

To determine migratory history in individual fish, ^{87}Sr/^{86}Sr ratios were examined in the outer (and presumed saltwater growth) region of the otolith. Fish were classified as ocean-rearing [anadromous] if the ^{87}Sr/^{86}Sr ratio integrated across a 40 µm (= 1 beam diameter) or larger transect fell within two standards errors (2SE) of the global marine value. Fish were classified as estuary-rearing [anadromous] if the integrated ^{87}Sr/^{86}Sr ratio exceeded the upper confidence limits of known freshwater signatures in the lower Klamath Basin (Figure 3), but fell below the standard for ocean-anadromy. Repeat migrants were identified by otolith ^{87}Sr/^{86}Sr ratios that alternated between freshwater and saltwater signatures. Finally, fish were classified as nonanadromous if the integrated ^{87}Sr/^{86}Sr ratio never exceeded the upper confidence limits of known freshwater signatures in the lower Klamath Basin.

To identify maternal origin, the methods of Zimmerman and Reeves (2002) were modified and adapted for use with strontium isotopes. Briefly, ^{87}Sr/^{86}Sr ratios were integrated across 80 µm transects in the core and freshwater growth regions of the otolith. Samples were omitted if the ablated transect missed the otolith core. Fish were determined to be progeny of an anadromous (steelhead) female parent if the ^{87}Sr/^{86}Sr ratio was significantly higher in the core region than in the freshwater growth region (1-tailed t-test, $\alpha = 0.05$). Conversely, fish were determined to be of nonanadromous (rainbow trout) maternal origin if this failed to be true. All calculations and statistical

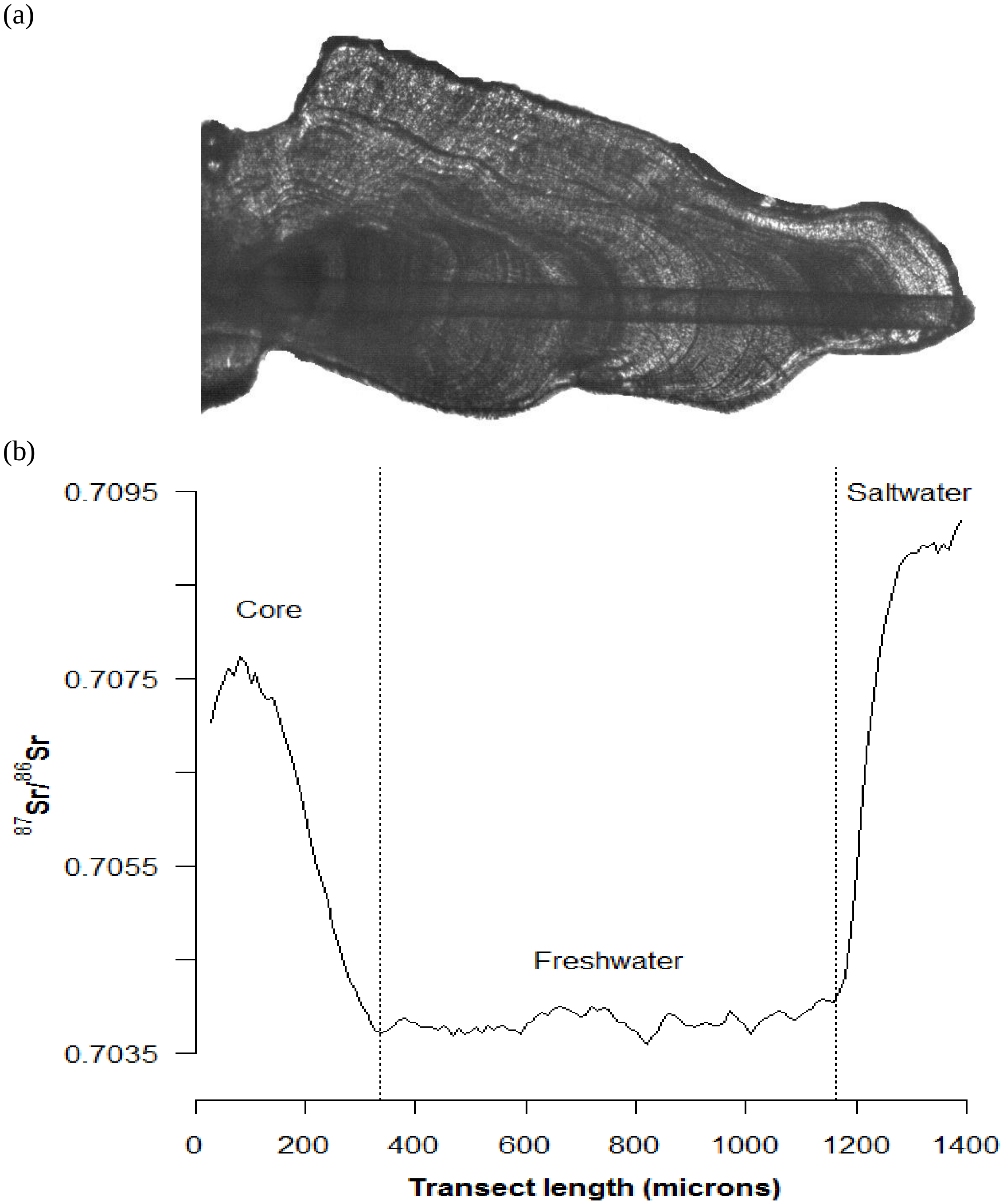

Figure 2. (a) Photo showing core-to-edge laser transect in sectioned otolith from half-pounder steelhead, and (b) corresponding ^{87}Sr/^{86}Sr ratios (integrated over 40 µm = one beam diameter) showing rise towards marine values (= 0.70918) in core and saltwater regions.

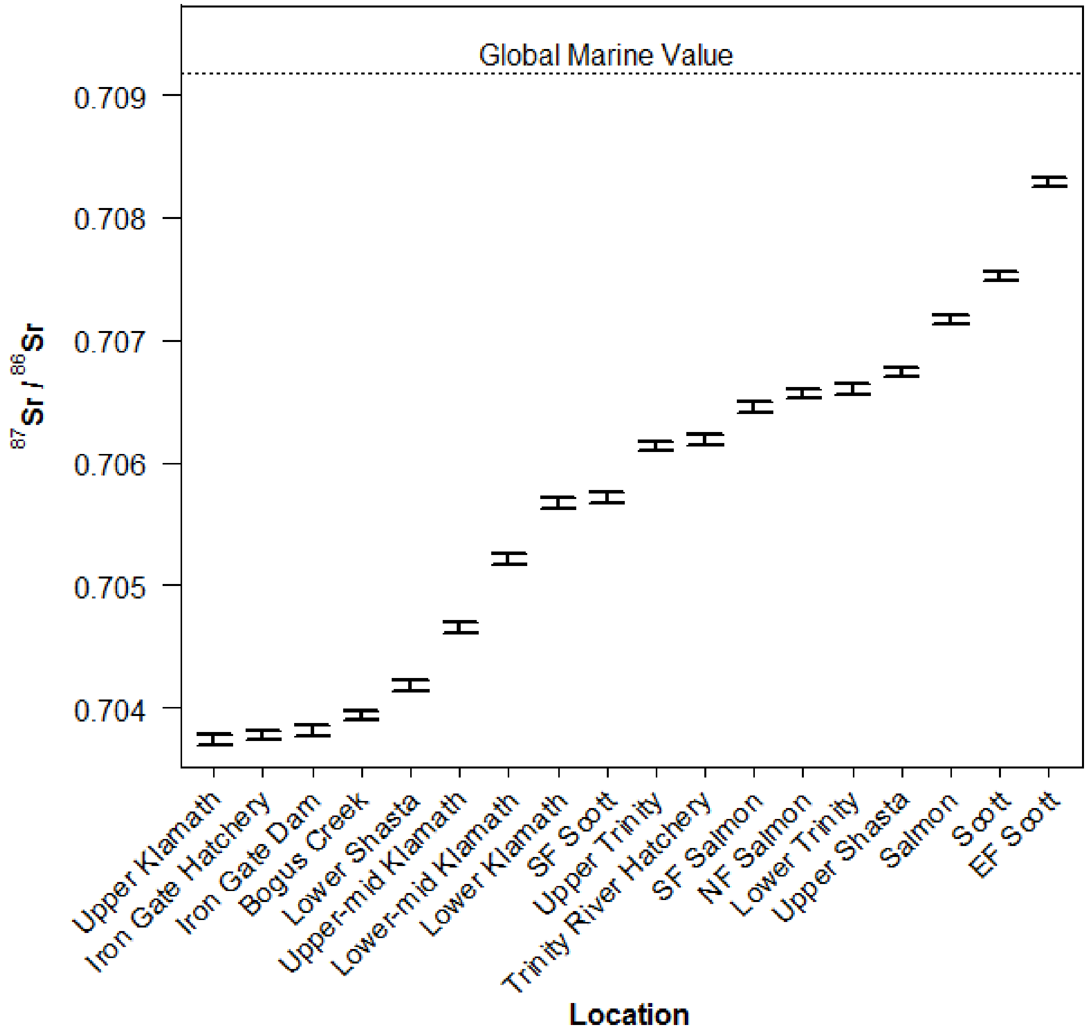

Figure 3. Strontium isotope ratios of water samples (mean ± 2SE) from the lower Klamath River Basin (Quiñones et al., unpublished data), and the global marine value with ^{87}Sr/^{86}Sr = 0.70918.

analyses were completed with the program R (R 2.10.1, Gentleman and Ihaka 1993).

Scale Preparation and Analysis

Scale samples were cleaned and then examined under a dissecting microscope to determine suitability for analysis. Samples that showed signs of significant regeneration or resorption were rejected. Suitable scales were mounted between two standard glass microscope slides, and one symmetrical and representative scale from each fish was photographed with a microscope-mounted digital camera.

Migratory history was first determined by subjective methods of visual scale examination. Briefly, freshwater growth was identified by narrow, tightly spaced circuli; and ocean growth was identified by thick, widely spaced circuli. Half-pounder migrations were identified by narrow, concentric bands of ocean and freshwater growth in the year of initial ocean entry; spawning events were identified by checking along the scale margins; and ocean annuli were identified by a tapered tightening of circuli in the absence of checking. Each fish was visually classified as anadromous or nonanadromous, and for steelhead, the number of anadromous (fresh-salt-fresh) migrations recorded.

To test the assumptions of scale pattern recognition, binary logistic regression was used to develop a model for predicting life history form (anadromous versus nonanadromous) based on objective, quantifiable scale characteristics. Because absolute or relative circuli spacing is typically the feature used to distinguish between freshwater and saltwater regions in scales, circulus increments were measured in the innermost and outermost regions of each representative sample. Scale photos were resized (4X) to maximize spatial resolution before a series of physical parameters were measured to the nearest µm along a line offset 15 degrees from the longitudinal axis of the scale (Figure 4) using image analysis software (Image Pro Plus, Media Cybernetics, Bethesda, Maryland). Variables were chosen to maximize the amount of available information that was generally common to all scale samples. Initial parameters included the mean, maximum, variance, and coefficient of variation of the circulus increment for the inner 13, 15, and 18 circuli; as well as for the outer 15, 18, 20, and 23 circuli. In addition, mean increment and variance ratios were calculated for each set of respective features in the inner and outer regions of the scale. Data were visually inspected, and parameters pertaining to the inner 18 circuli and outer 23 circuli were omitted upon discovery that these features were not common to the entire data set. Relationships between the remaining scale parameters and life history form were then evaluated qualitatively through examination of bivariate scatter plots and boxplots, and evaluated quantitatively through calculation of the Mahalanobis distance (Mahalanobis 1936). Parameters with the greatest discriminatory power were screened to maximize the contrast between groups, while eliminating sources of non-independence. The remaining variables were entered into a series of candidate binary logistic regression models, which were ranked according to predictive accuracy and fit. Model accuracy was evaluated by comparing predicted classifications of life history form to a priori classifications, and model fit was evaluated using Akaike's information criterion (AIC, Aikaike 1974).

Reader accuracy was assessed by comparing a priori determinations of migratory history to those results obtained during visual scale examination. Next, results from

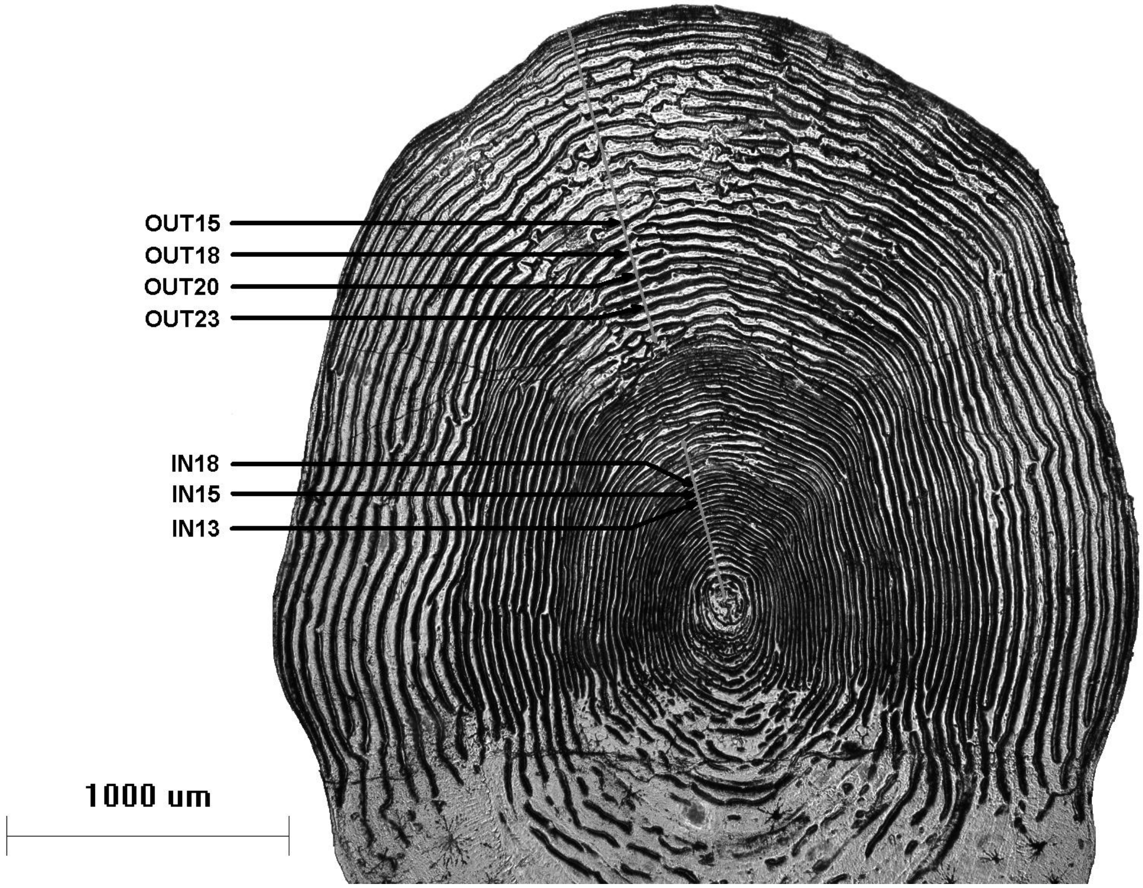

Figure 4. Photo of half-pounder scale indicating the distal margins of the inner 13, 15, and 18 circuli (IN13, IN15, and IN18) in the freshwater region; and the medial margins of the outer 15, 18, 20, and 23 circuli (OUT15, OUT18, OUT20, and OUT23) in the saltwater region.

qualitative and quantitative scale analysis were compared to determine if one method was significantly more accurate in identifying life history form (Binomial Proportions Test (BPT), α = 0.05). To distinguish between reader error and inaccurate assumptions of scale pattern recognition, results were carefully examined to identify instances in which both methods of scale analysis failed to correctly classify fish by life history form.

Determination of Age, Growth, and Life History

After the initial training and validation phase was complete, scales were visually examined and measured with image analysis software to determine age, growth, and life history of fish captured throughout the basin. First, scales were cleaned, prepared, and photographed according to the procedures outlined in the preceding section. Next, scale landmarks indicative of fresh and salt annuli, movement between fresh and salt environments, and spawning events were identified (Figure 5). Then distances between landmarks and the focus of the scale were measured to the nearest µm along a transect offset 15° from the longitudinal axis of the scale. Finally, lengths at life history landmarks, and growth increments between landmarks, were back-calculated to the nearest mm using the Fraser-Lee method (Fraser 1916; Lee 1920; Carlander 1982). An in-basin standard for the biological intercept (30.0 mm, Hopelain 1998) was adopted to minimize the variance created by different scale readers (Carlander 1982). Scales that presented difficult patterns during the first examination were analyzed a second time several weeks later. In the event that the life history could still not be confidently determined, a second qualified reader analyzed the scale. Scales were then included for

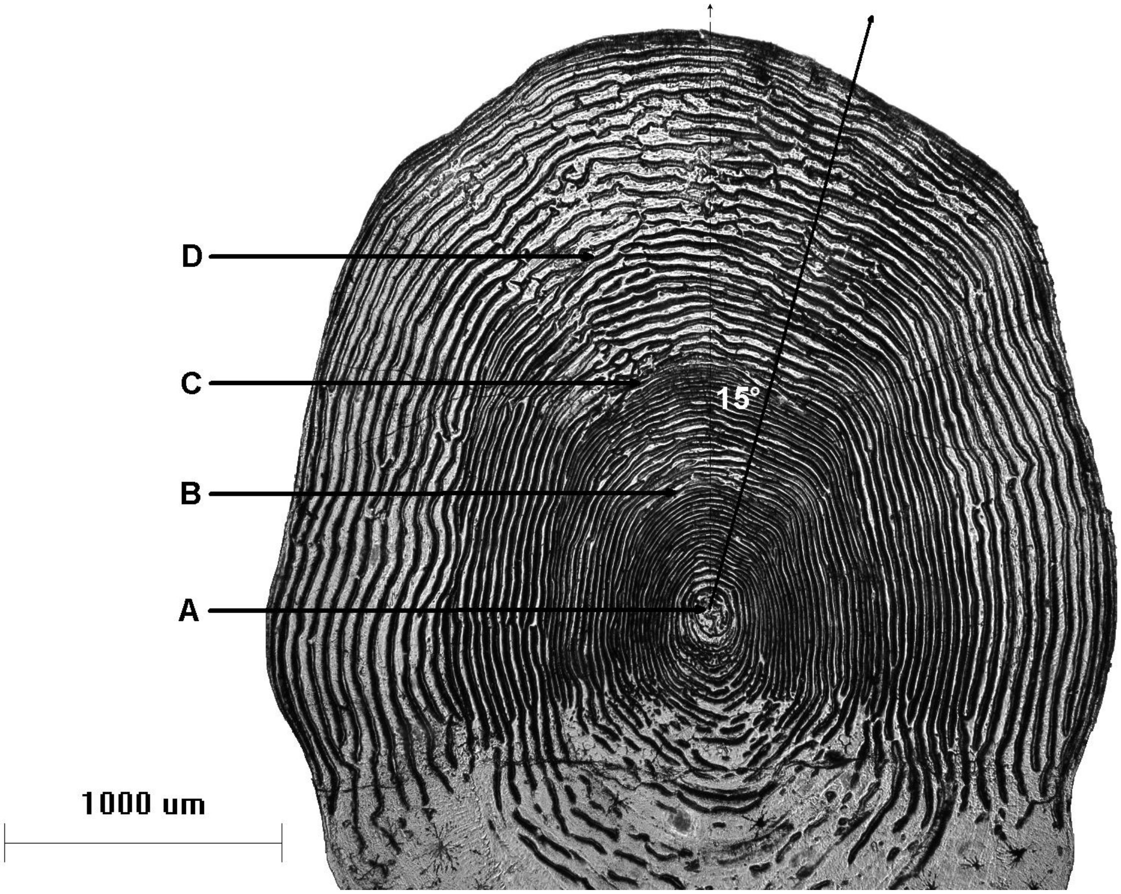

Figure 5. Photo of half-pounder scale indicating focus (A), first freshwater annulus (B), second freshwater annulus (C),point of ocean entry (D), and 15° offset from longitudinal axis.

data analysis if readers reached a consensus, and omitted if readers failed to reach a consensus. Nonanadromous fish were classified as residents if length at capture exceeded the 95th percentile for length at ocean entry (298mm), or if age at capture exceeded the maximum recorded age at ocean entry (3 years). If nonanadromous fish were both smaller than 298 mm and no older than 3 years at capture, life history was deemed “unknown”, and these fish were excluded from further analysis. I defined half-pounders as anadromous fish (i.e., steelhead) that migrate back into freshwater in the year of initial ocean entry (i.e., sea at capture = 1 year). Steelhead were classified as adults if sea age at capture was greater than 1 year, and approaching at least 2 years. Life history was reported according to the notation presented by Hopelain (1998). Life history categories were distinguished by number of years spent rearing in freshwater, presence or absence of a half-pounder migration, number of years in saltwater, and number of spawning migrations. Reported ages of fish captured in fall or early winter included the subsequent winter annulus. Examples of the life history notation system are presented in Table 1. Because resorption or “checking” of scale material can lead to positive bias in back-calculation of lengths, only fish with fewer than two spawning checks were used to generate retrospective length-at-age data. To identify temporal changes in life history structure, results from this study were contrasted with those of Hopelain (1998). Incidence rates were compared with the binomial proportions test (BPT, $\alpha = 0.05$).

Half-Pounder Maturity

To determine sex and incidence of maturity in half-pounders, a sub-sample of fish

Table 1. Examples of the notation system (Hopelain 1998) used to report life history. A backward slash (/) separates years in freshwater (left) from years in saltwater (right), and a period (.) separates growing years from spawning years. A lowercase *h* denotes a half-pounder run, and a lowercase *s* denotes a spawning run. For fish captured in fall or early winter, the reported age includes the subsequent winter annulus.

		Saltwater age (years)				
Description	Freshwater age (years)	Half-pounder	Growth	Spawn	Total age (years)	Notation
Resident	5				5	5/
Half-pounder	2	1			3	2/h
Adult steelhead	3	1	1	1	6	3/h.1.1s
Adult steelhead	2	1		1	4	2/h.1s
Adult steelhead	2		1	2	5	2/1.2s

was sacrificed in a time and size stratified manner. After scales and biological data were collected in the field, fish were weighed to the nearest gram. Fish were then tagged and immediately placed on ice for transport to the laboratory. Gonads were extracted and weighed to the nearest 0.01 g, and sex and maturity assessed. Immature males were identified by smooth, spindly gonads; immature females by gonads with an anterior thickening, triangular cross-section, and granular appearance; mature males by testes that were white, visibly enlarged, and exceeded 1.00 g in combined weight; and mature females by ovaries with visibly developed eggs and a combined weight exceeding 1.00 g (Kesner and Barnhart 1972). In the event that a confident sex determination could not be made during a visual inspection, gonads were examined under a dissecting microscope (3X) to confirm the presence or absence of developing oocytes.

Based on initial examination of the data, a number of biological parameters were included in analysis of factors related to incidence of maturity in half-pounders, the relative importance of which were assessed by comparing candidate models. The initial suite of variables included length, weight, condition factor ($w \cdot l^{-3} \cdot 10^{5}$), age, sex, and growth (change in length). Data were inspected for relationships among variables and for relationships between variables and incidence of maturity. To identify these relationships, I examined bivariate boxplots and scatter plots, regression plots, interaction plots, and results tables from one-way analysis of variance (ANOVA). Predictive variables with no effect were dropped from consideration, as were redundant or confounding parameters. Next, the remaining continuous and categorical parameters (Table 2) were used to construct a series of candidate binary-response models. Candidate

Table 2. Description and summary statistics for variables used in modeling incidence of maturity in half-pounders.

Variable	Description	Mean ± SE	Range
FLFW	Fork length at last freshwater annulus* (mm)	150 ± 4	71 - 296
FLOE	Fork length at ocean entry (mm)*	216 ± 4	131 - 337
FLFWRE	Fork length at freshwater re-entry* (mm)	321 ± 4	253 - 449
COND	Condition factor at capture ($w \cdot l^{-3} \cdot 10^5$)	1.17 ± 0.01	0.89 - 1.55
AGE	Smolt age (years)	1.93 ± 0.06	1.0 - 3.0
SEX	Sex (male = 1, female = 2)	1.54 ± 0.05	1.0 - 2.0

*Back-calculated during scale analysis

models, including interaction and main effect terms, were simplified in a stepwise procedure and ranked according to fit using AIC. An empirically derived “best” model was identified based on explanatory power, parsimony, and significance. Finally, the best fitting model was used to generate maturation probabilities.

Fecundity

To quantify the relationship between female size and fecundity in Klamath steelhead, biological data were collected from sexually mature females. In order to minimize the impact on the wild population, most samples were collected from artificially spawned fish captured at the Trinity River Hatchery in January-February 2008 (See Figure1). Hatchery fish were measured to the nearest cm and air-spawned into 1.9 L buckets before they were released back into the river. Eggs were water hardened for 30 minutes in an iodide solution and total ovarian volume was measured to the nearest 0.25 fl oz (1 fl oz = 29.57 ml). Egg number was counted in volumetric subsamples, and then used to estimate total fecundity. Accuracy of this estimation technique was evaluated by comparing volumetric approximations to hand counted values in approximately 10% of the samples (paired t-test, $\alpha = 0.05$). After data were $\log_e$ transformed to meet the assumptions of linearity and homogeneity of variance, total ovarian volume and fecundity were regressed on length.

I evaluated the fit of wild fish to the hatchery derived model by comparing the length-fecundity relationships of naturally and artificially propagated steelhead. To collect fecundity data from wild fish, a small number of maturing females were sacrificed. After being measured and weighed in the field, wild fish were immediately placed on ice for transport to the laboratory. Once in the lab, skeins were removed and weighed to the nearest 0.01g. Gravimetric sub-samples were removed from complete skeins and placed in modified Gilson's solution for a period of one to four weeks, or until eggs were loose or easily removed from the ovarian membrane (Friedland et al. 2005). Once loose, eggs were rinsed and drained (0.63 µm sieve), and sub-samples were hand counted to estimate total fecundity. Data were $\log_e$ transformed and plotted against the existing length-fecundity regression model.

Influencing Factors and Consequences of Life History Trajectories

To explore the influencing factors and consequences of specific *O. mykiss* trajectories, I compared the age, length, growth, and reproductive history of fish exhibiting alternative life history pathways. Attributes were compared between anadromous and nonanadromous individuals to identify factors associated with residualization, and were further compared to identify proximate fitness consequences of leading a resident vs. migratory life. To isolate the influencing factors and consequences of the half-pounder life history, comparisons focused on identifying differences between steelhead exhibiting "parallel" life history trajectories (i.e., pathways that differed only in the presence or absence of a half-pounder stage). Groups were compared statistically with ANOVA and two-sample t-tests ($\alpha = 0.05$). To identify potential fecundity-related fitness costs of specific life history trajectories, egg number was estimated using the empirically derived regression model.

RESULTS

Fish Capture and Data Collection

Sampling effort and size distribution of specimens varied among sub-basins (Table 3; Figure 6). More than half (53%) of the fish sampled were captured with hook and line, and the remainder were captured at CDFG weir trapping facilities. Scales and biological data were collected from 244 and 61 fish trapped on the Trinity River in 2007 and 2008, representing approximately 3.3% and 1.1% of the estimated wild adult runs in that sub-basin, respectively (Sinnen 2009, personal communication). Sub-basin of origin was unknown for fish captured in the mainstem Klamath; however, approximately 97% of these fish were captured upstream of the Trinity confluence, suggesting that a similar proportion originated upstream of the Trinity.

Validation of Scale Analysis

Otolith Microchemistry: Migratory History and Maternal Origin

The relationship between maternal origin and migratory history differed among individuals. A total of 65 otoliths were analyzed to determine migratory history and maternal origin**,** of which, two were excluded from further analysis upon discovery of vateritic structure. Of the remaining 63 fish, 5 were classified as resident rainbow trout (fork length: 392-465 mm) and 58 were classified as steelhead (fork length: 257-669 mm). Of the steelhead, 54 fish were categorized as half-pounders (52 ocean-rearing, 2 estuary-rearing), and four fish were categorized as adults and repeat migrants (all had

Table 3. Location, method, and time of capture; as well as sample size, mean ± 1SE fork length, and sex ratio (male to female (M : F)) for *Oncorhynchus mykiss* sampled in the lower Klamath River Basin.

River	Collection method	Collection Dates	n	FL ± SE (mm)	M : F
Klamath	Hook and line	Aug 2007-Apr 2009	251	399 ± 6	0.8 : 1.0
Trinity	Weir, hook and line	Aug 2007-Nov 2008	326	595 ± 5	0.9 : 1.0
Salmon	Hook and line	Nov 2008-Mar 2009	39	426 ± 22	0.6 : 1.0
Scott	Hook and line	Oct 2008-Nov 2008	21	438 ± 14	1.0 : 1.0
Shasta	Weir	Oct 2008-Dec 2008	18	479 ± 17	0.4 : 1.0

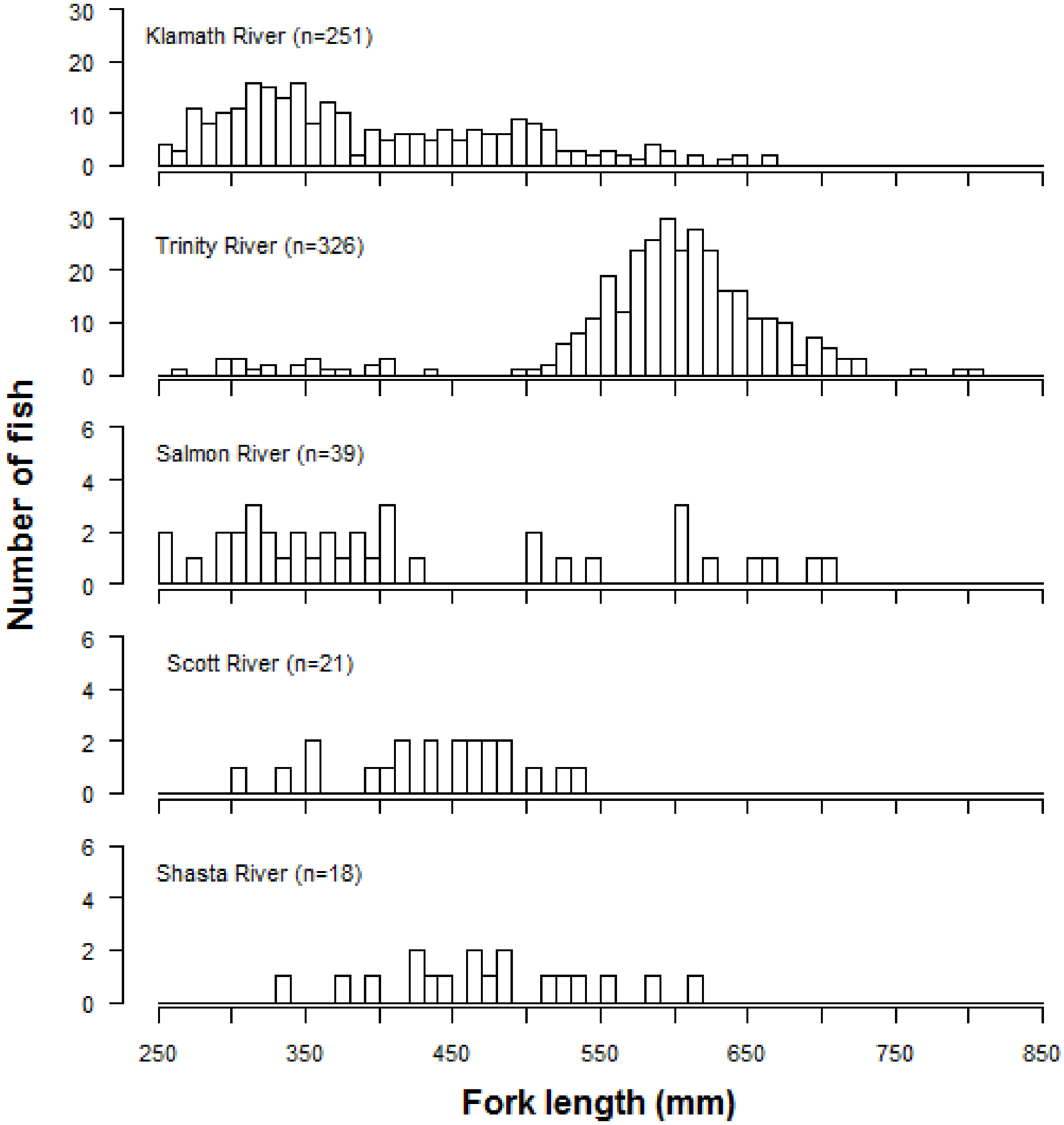

Figure 6. Size distribution of *Oncorhynchus mykiss* sampled in the lower Klamath River Basin from 2007 through 2009. Sample sizes are given in parenthesis.

previously retuned as half-pounders). Representative otolith transects for each life history type are shown in Figures 7 and 8. Of the five rainbow trout, one was classified as progeny of rainbow trout, two were classified as steelhead progeny, and two were classified as "unknown" because maternal origin could not be confidently determined. Of the 58 steelhead, 37 were classified as steelhead progeny, 12 were classified as progeny of rainbow trout, and nine were classified as unknown. Representative core-to-edge otolith transects for each combination of maternal origin and migratory history are shown in Figure 9.

Scale Analysis

Methods of qualitative scale analysis resulted in the correct classification of life history form in approximately 95% (59 of 62) of fish, and resulted in the correct identification of lifetime migratory history in approximately 94% (58 of 62) of fish. Visual methods resulted in three misclassifications of life history form (one false anadromous and two false nonanadromous) and four misclassifications of lifetime migratory history. Of the four misclassifications of migratory history, three were due to misidentification of life history form, and one resulted from the misidentification of an ocean annulus as a spawning check.

Quantitative scale pattern analysis accurately predicted life history form in approximately 97% (59 of 61) of the individuals from which otoliths were analyzed. Of the scale parameters evaluated, the mean circulus increment for the outer 20 circuli provided the greatest power to correctly discriminate between anadromous and

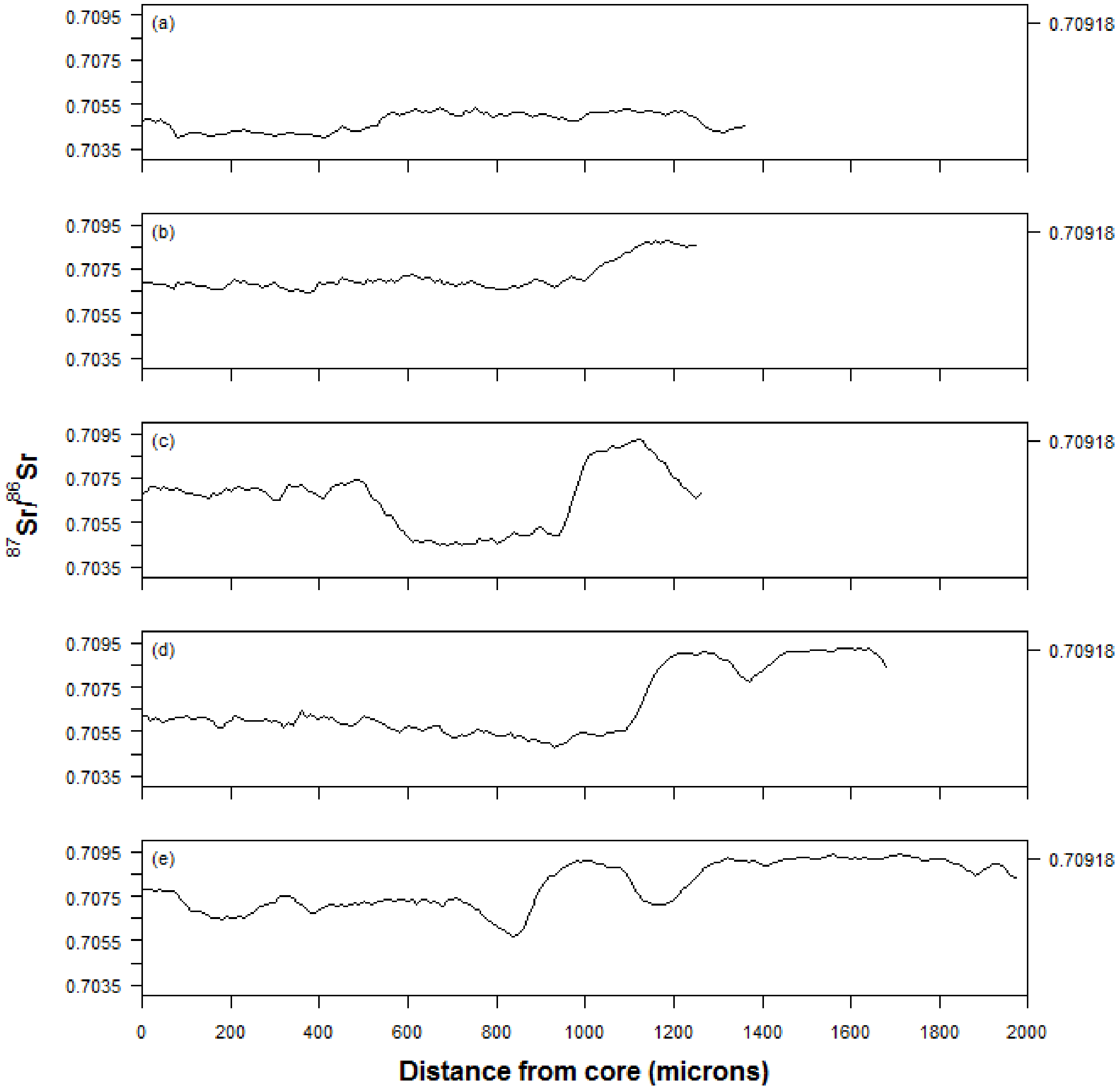

Figure 7. Otolith ^{87}Sr/^{86}Sr transects from (a) a resident rainbow trout, (b) an estuary-rearing half-pounder, (c) an ocean-rearing half-pounder, (d) an adult steelhead that made a half-pounder migration and returned to spawn in the following winter, and (e) an adult steelhead that made a half-pounder migration and returned to spawn after two ocean winters.

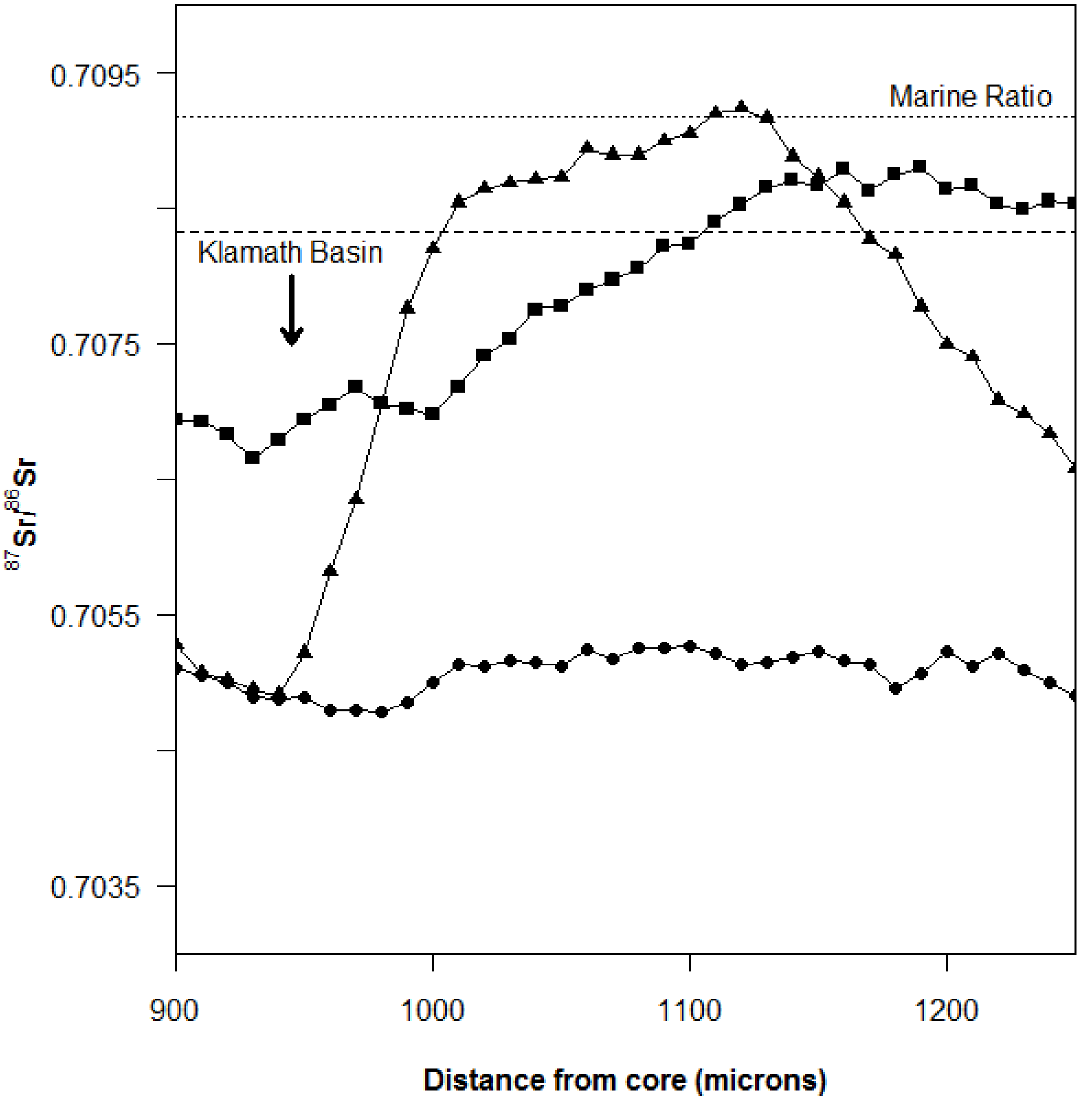

Figure 8. Otolith ^{87}Sr/^{86}Sr transects from the outer regions of a resident rainbow trout (circles), estuary-rearing half-pounder (squares), and ocean-rearing half-pounder (triangles). Horizontal lines represent the upper bounds of known $^{87}Sr/^{86}Sr$ ratios in the lower Klamath River Basin (dashed line), and the global marine value (= 0.70918; dotted line).

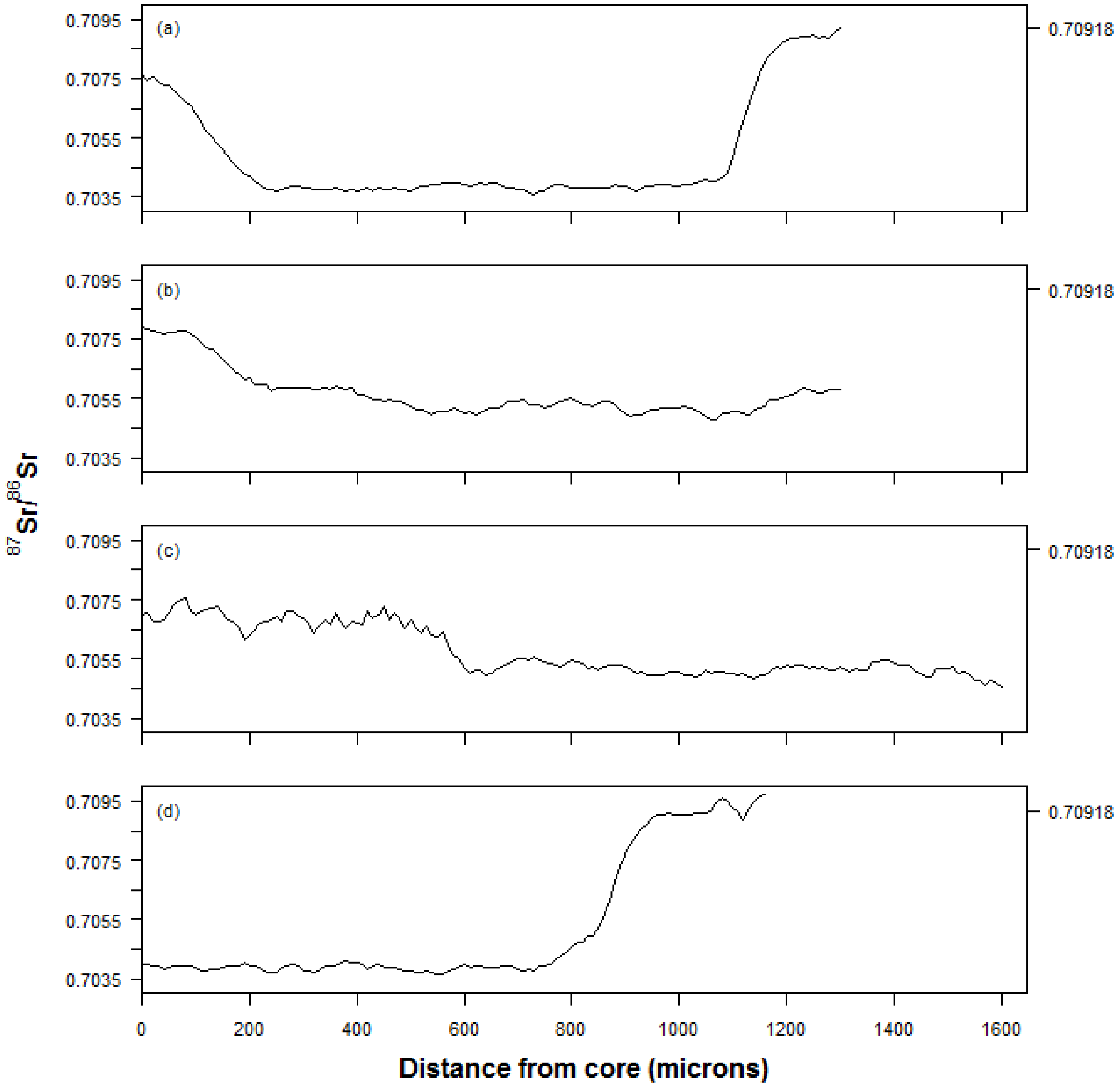

Figure 9. Representative core-to-edge otolith transects from *Oncorhynchus mykiss* classified by the following combinations of maternal origin and migratory history: (a) anadromous/anadromous (b) anadromous/nonanadromous (c) nonanadromous/nonanadromous and (d) and nonanadromous/anadromous.

nonanadromous fish ($z = 2.10$, $P = 0.036$). Addition of a variance ratio (outer 20 circuli to inner 15 circuli) to the regression model increased the classification accuracy from 95 to 97%. Quantitative methods resulted in two misclassifications of life form: one false anadromous and one false nonanadromous.

Overall, methods of qualitative and quantitative scale analysis showed 95% agreement in predicting life history form, and there was no difference in predictive accuracy between methods ($\chi^2 \approx 0.0$, df =1, n =123, $P \approx 1.0$). Of the three fish misclassified by visual methods, one was also misclassified by the best fitting logistic regression model; and of the two fish misclassified by the model, one was correctly classified by visual methods. All of the misclassifications of life form were associated with scales in which the spacing of the outermost 20 circuli fell in a narrow band of overlap between anadromous and nonanadromous fish (29-32 µm).

As a result of this preliminary analysis, I created an objective rule to help guide future determinations of life history form. In the event that a fish could not be confidently classified during visual analysis, the mean circulus increment for the outer 20 circuli was calculated from a representative scale. If the mean value was greater than 30 µm, a fish was classified as anadromous. Conversely, if the mean value was less than 30 µm, a fish was classified as nonanadromous. When this simple rule was applied to the original training set a posteriori, 97% of fish were classified to the correct group.

Age, Growth, and Life History

Proportions of fish classified by life history were highly variable among sub-basins (Table 4; Appendix A). Through visual examination of scales, a total of 32 life history categories were observed in *O. mykiss* from the Klamath, Trinity, Salmon, Scott, and Shasta Rivers (Table 5). At least 30 of those categories represented potential maturation trajectories (i.e., developmental pathways by which a fish spawns). Further, inclusion of logical intermediates between observed categories suggests that *O. mykiss* in the lower Klamath River Basin may exhibit at least 33 different life history categories at maturity (Figure 10).

For rainbow trout and juvenile steelhead, freshwater age and growth varied within and among sub-basins. Because sample sizes of trout from individual sub-basins were small, data were pooled to allow examination of residents (Table 6). Age of trout ranged from 2 to 6 years (mean ± SE = 3.60 ± 0.13 years), and length of trout ranged from 268 to 508 mm (mean ± SE = 384 ± 9 mm). Annual growth rates for residents ranged from 27 to 225 $\text{mm}\cdot\text{year}^{-1}$ (mean ± SE = 103 ± 3 $\text{mm}\cdot\text{year}^{-1}$). Among steelhead, smolt age ranged from 1 to 3 years (mean ± SE = 1.92 ± 0.02 years; Table 7), and smolt length ranged from 112 to 394 mm (mean ± SE = 216 ± 2 mm; Table 8). Freshwater growth rates for juvenile steelhead ranged from 23 to 229 $\text{mm}\cdot\text{year}^{-1}$ (mean ± SE = 86 ± 1 $\text{mm}\cdot\text{year}^{-1}$; Table 9). In general, smolt age was negatively related to length at age, but positively related to smolt length. In other words, slow growing fish typically remained in freshwater longer, and entered the ocean at greater size than faster growing fish.

Half-pounders were captured continuously in the lower Klamath River Basin from August through April, with peak numbers generally occurring in the mainstem Klamath during September and October. Length at capture ranged from 256 to 525 mm (mean ±

Table 4 Percentage of *Oncorhynchus mykiss* that were classified by life history as nonanadromous (residents, “unknown”), anadromous (half-pounders, adults), and “indeterminable” from collections made in the lower Klamath River Basin in 2007-2009. Nonanadromous fish were classified as residents if length at capture exceeded the 95th quantile for length at ocean entry (298mm), or if age at capture exceeded the maximum recorded age at ocean entry (3 years). If nonanadromous fish were both smaller than 298 mm and no older than 3 years at capture, life history was deemed “unknown”, and these fish were excluded from further analysis. Anadromous fish (i.e., steelhead) were classified as half-pounders if sea age at capture was equal to 1 year, and classified as adults if sea age at capture was greater than 1 year and approaching at least 2 years. If readable scales were unavailable, life history was deemed “indeterminable”.

		Life history (%)				
		Nonanadromous		Anadromous		
River	n	Residents	Unknown	Half-pounders	Adults	Indeterminable
Klamath*	251	7.2	2.4	62.5	25.1	2.8
Trinity	326	1.2	0.3	5.5	89.3	3.7
Salmon	39	20.5	5.1	46.2	28.2	0.0
Scott	21	57.2	0.0	14.3	19.0	9.5
Shasta	18	5.6	0.0	50.0	44.4	0.0
All	655	6.6	1.4	31.2	57.6	3.2

*Note: 97% of fish were captured upstream of the Trinity confluence.

Table 5. Sample size and mean ± SE fork length (at capture) for life history categories observed in *Oncorhynchus mykiss* from the lower Klamath River Basin. Life history was reported according to the notation system presented by Hopelain (1998). A backward slash (/) separates years in freshwater (left) from years in saltwater (right), and a period (.) separates growing years from spawning years. A lowercase *h* denotes a half-pounder run, and a lowercase *s* denotes a spawning run. For fish captured in fall or early winter, the reported age includes the subsequent winter annulus. Plus signs (+) indicate whether the life history category was observed in the Klamath (KLM), Trinity (TRN), Salmon (SAL), Scott (SCT), and Shasta (SHA) Rivers.

			Presence/Absence 2007-2009				
Life history category			River				
	n	FL ± SE (mm)	KLM	TRN	SAL	SCT	SHA
Nonanadromous							
2/	1	360		+			
3/	23	364 ± 9	+	+	+	+	
4/	12	390 ± 22	+	+	+	+	+
5/	5	436 ± 14	+		+	+	
6/	1	508			+		
Anadromous							
1/h	33	305 ± 6	+	+	+		
1/h.1s	17	513 ± 15	+	+			+
1/h.2s	5	587 ± 26		+			
1/h.3s	1	609			+		
1/h.1.1s	8	634 ± 23	+	+			
1/h.1.4s	1	700			+		
1/h.2.1s	1	669			+		
1/1.1s	25	595 ± 6		+		+	
1/1.2s	5	648 ± 16		+			
1/2.1s	2	755 ± 45		+			
2/h	138	360 ± 5	+	+	+	+	+
2/h.1s	40	511 ± 8	+	+	+	+	+
2/h.2s	10	574 ± 9	+	+			+
2/h.3s	2	643 ± 3	+	+			
2/h.1.1s	4	633 ± 23		+	+		
2/h.1.2s	1	640		+			
2/1.1s	172	604 ± 3	+	+	+		
2/1.2s	16	640 ±9		+	+		
2/1.3s	5	686 ±13		+	+		
2/2.1s	11	707 ± 15		+			
2/2.2s	2	715 ± 15		+			
3/h	31	405 ± 12	+	+	+		+

Table 5. Sample size and mean ± SE fork length (at capture) for life history categories observed in *Oncorhynchus mykiss* from the lower Klamath River Basin. Life history was reported according to the notation system presented by Hopelain (1998). A backward slash (/) separates years in freshwater (left) from years in saltwater (right), and a period (.) separates growing years from spawning years. A lowercase *h* denotes a half-pounder run, and a lowercase *s* denotes a spawning run. For fish captured in fall or early winter, the reported age includes the subsequent winter annulus. Plus signs (+) indicate whether the life history category was observed in the Klamath (KLM), Trinity (TRN), Salmon (SAL), Scott (SCT), and Shasta (SHA) Rivers (continued).

			Presence/Absence 2007-2009				
Life history category			River				
	n	FL ± SE (mm)	KLM	TRN	SAL	SCT	SHA
Anadromous							
3/h.1s	5	518 ± 8	+	+			
3/h.2s	1	615	+				
3/1.1s	13	603 ± 13		+	+		
3/1.3s	2	620 ± 10		+			
3/2.1s	1	640		+			

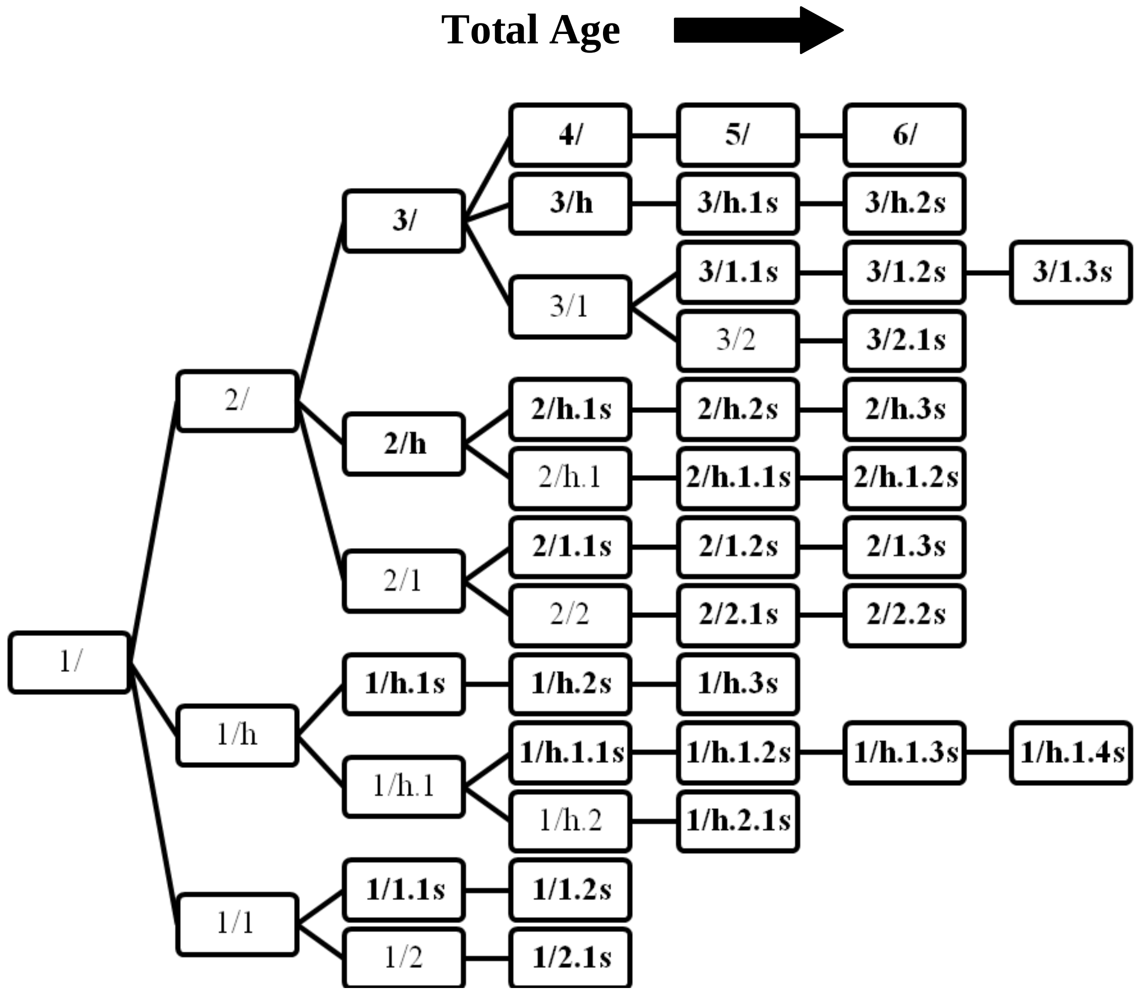

Figure 10. Life history pathways observed in *Oncorhynchus mykiss* from the lower Klamath River Basin in 2007-2009. Life history was reported according to the notation system presented by Hopelain (1998). A backward slash (/) separates years in freshwater (left) from years in saltwater (right), and a period (.) separates growing years from spawning years. A lowercase *h* denotes a half-pounder run, and a lowercase *s* denotes a spawning run. For fish captured in fall or early winter, the reported age includes the subsequent winter annulus. Life history categories highlighted in bold represent observed spawning trajectories (i.e., pathways by which a fish attains maturity).

Table 6. Mean ± 1SE fork length and growth at age for rainbow trout captured in the lower Klamath River basin in 2007-2009 (n = 43).

	FL (mm)					
Age	1	2	3	4	5	6
2	119	NA				
3	112 ± 4	235 ± 11	347 ± 18			
4	95 ± 6	170 ± 12	300 ± 15	335 ± 33		
5	95 ± 12	182 ± 22	308 ± 22	385 ± 22	423 ± 16	
6	121	195	331	425	480	508
All	106 ± 3	209 ± 9	312 ± 10	368 ± 19	434 ± 17	508

	Growth (mm)					
	0-1	1-2	2-3	3-4	4-5	5-6
2	119	NA				
3	112 ± 4	123 ± 9	103 ± 17			
4	95 ± 6	75 ± 9	131 ± 14	74 ± 21		
5	95 ± 12	87 ± 16	126 ± 14	77 ± 16	59 ± 13	
6	121	74	136	94	55	28
All	106 ± 3	103 ± 7	124 ± 8	77 ± 11	58 ± 10	28

Table 7. Summary of smolt age for all steelhead sampled in the lower Klamath River basin in 2007-2009 (U = unknown).

		Smolt age (%)			
River	n	1	2	3	U
Klamath	220	20.0	61.8	12.7	5.5
Trinity	309	15.2	73.1	6.5	5.2
Salmon	29	17.2	72.4	7.0	3.4
Scott	7	14.7	85.7	0.0	0.0
Shasta	17	5.9	70.6	17.6	5.9
Total	582	16.9	68.9	9.1	5.1

Table 8. Mean ± 1SE fork length at age for juvenile steelhead from the lower Klamath River Basin, as categorized by river of capture (OE = ocean entry; n = 561).

		FL (mm)			
River	Smolt Age	1	2	3	OE
Klamath	1	107 ± 3			186 ± 5
	2	91 ± 1	174 ± 4		234 ± 4
	3	85 ± 3	156 ± 8	222 ± 11	254 ± 12
	All	94 ± 1	171 ± 4	222 ± 11	226 ± 4
Trinity	1	117 ± 3			194 ± 5
	2	89 ± 1	166 ± 2		205 ± 2
	3	82 ± 3	132 ± 5	190 ± 9	215 ± 9
	All	93 ± 1	164 ± 2	190 ± 9	203 ± 2
Salmon	1	111 ± 7			199 ± 8
	2	91 ± 3	152 ± 6		224 ± 5
	3	107 ± 11	168 ± 18	227 ± 11	259 ± 4
	All	95 ± 3	154 ± 5	227 ± 11	222 ± 5
Scott	1	91			214
	2	96 ± 7	224 ± 31		272 ± 25
	3				
	All	95 ± 6	224 ± 31		263 ± 23
Shasta	1	105			190
	2	103 ± 4	203 ± 18		261 ± 14
	3	101 ± 9	166 ± 28	316 ± 11	329 ± 16
	All	103 ± 3	195 ± 15	316 ± 11	269 ± 14
All	1	112 ± 2			191 ± 3
	2	90 ± 1	170 ± 2		219 ± 2
	3	86 ± 2	149 ± 5	216 ± 8	245 ± 8
	All	94 ±1	168 ± 2	216 ± 8	216 ± 2

Table 9. Mean growth ± 1SE for juvenile steelhead from the lower Klamath River Basin (n = 539). "Plus growth" is defined as the increment of length accrued between the last freshwater annulus and ocean entry.

		Growth (mm)			
River	Smolt Age	0-1	1-2	2-3	Plus
Klamath	1	107 ± 3			79 ± 5
	2	91 ± 1	83 ± 3		61 ± 3
	3	85 ± 3	71 ± 6	66 ± 6	32 ± 6
	All	94 ± 1	80 ± 3	66 ± 6	61 ± 2
Trinity	1	117 ± 3			77 ± 4
	2	89 ± 1	77 ± 2		39 ± 2
	3	82 ± 3	51 ± 4	58 ± 6	25 ± 5
	All	93 ± 1	75 ± 2	58 ± 6	45 ± 2
Salmon	1	111 ± 7			88 ± 4
	2	91 ± 3	61 ± 4		71 ± 6
	3	107 ± 11	61 ± 7	60 ± 8	31 ± 6
	All	95 ± 3	61 ± 3	60 ± 8	70 ± 5
Scott	1	91			123
	2	96 ± 7	128 ± 29		48 ± 15
	3				
	All	95 ± 6	128 ± 29		59 ± 17
Shasta	1	105			84
	2	103 ± 4	100 ± 16		58 ± 10
	3	101 ± 9	65 ± 30	150 ± 40	13 ± 7
	All	103 ± 3	93 ± 14	150 ± 40	51 ± 9
All	1	112 ± 2			79 ± 3
	2	90 ± 1	80 ± 2		49 ± 2
	3	86 ± 2	63 ± 4	68 ± 5	28 ± 4
	All	94 ± 1	78 ± 2	68 ± 5	52 ± 1

SE = 358 ± 4 mm), and weight at capture ranged from 172 to 986 g (mean ± SE = 426 ± 17 g). For steelhead that exhibited the half pounder life history, mean smolt age was 1.90 years (SE = 0.03); and of the 245 fish for which sex could be determined (n = 353), 116 were male and 129 were female. Length at ocean entry ranged from 112 to 394 mm, length at freshwater re-entry ranged from 247 to 490 mm, and length at the end of the first saltwater winter ranged from 257 to 525 mm (Table 10). For half-pounders, growth between the time of ocean entry and freshwater re-entry ranged from 48 to 224 mm, and growth between the time of freshwater re-entry and the end of the first saltwater winter ranged from 0 to 62 mm. Overall, growth between the time of ocean entry and the end of the first saltwater winter ranged from 73 to 261 mm.

Ocean age and growth, as well as reproductive history, were highly variable among steelhead. Length of steelhead ranged from 257 to 626 mm at the end of the first saltwater winter, from 380 to 730 mm at the end of second saltwater winter, from 480 to 810 mm at the end of third saltwater winter, and from 640 to 730 mm by the end of fourth saltwater winter (Table 11). Excluding half-pounders, steelhead in their first year at sea grew from 92 to 400 mm (mean ± SE = 288 ± 3 mm) between the time of ocean entry and the formation of the first salt annulus. Both incidence of the half-pounder life history and incidence of repeat spawning were inconsistent among sub-basins (Table 12). Of the repeat spawners observed, more than half (56.9%) were female.

Comparisons of current and historic data suggest that the structure of *O. mykiss* life histories in the lower Klamath River Basin has changed over time (Table 12). Resident rainbow trout comprised of approximately 6.6% of all *O. mykiss* sampled in

Table 10. Mean ± 1SE fork length and growth of half-pounders from the lower Klamath River Basin at (or between) ocean entry (OE), freshwater re-entry (FWRE), and first saltwater winter (1SW; n = 288).

	FL (mm)		
Smolt Age	OE	FWRE	1SW
1	184 ± 4	296 ± 3	327 ± 5
2	232 ± 4	330 ± 3	366 ± 6
3	259 ± 10	355 ± 11	414 ± 20
All	225 ± 3	323 ± 3	357 ± 4
	Growth (mm)		
	OE-FWRE	FWRE-1SW	OE-1SW
1	114 ± 5	28 ± 2	148 ± 7
2	108 ± 3	27 ± 1	140 ± 5
3	124 ± 10	27 ± 7	173 ± 14
All	111 ± 2	27 ± 1	145 ± 3

Table 11. Mean ± 1SE fork length and growth of steelhead from the lower Klamath River Basin at sea (OE = ocean entry, SW = saltwater winter; n = 401).

	FL (mm)			
Smolt age	1SW	2SW	3SW	4SW
1	386 ± 9	559 ± 8	637 ± 15	669
2	462 ± 5	582 ± 4	642 ± 9	690 ± 27
3	458 ± 15	551 ± 29	628 ± 13	NA
All	445 ± 4	575 ± 4	638 ± 7	685 ± 19
	Growth (mm)			
	OE – 1SW	1SW-2SW	2SW-3SW	3SW-4SW
1	197 ± 9	161 ± 7	80 ± 5	40
2	250 ± 5	114 ± 3	67 ± 4	35 ± 7
3	235 ± 14	116 ± 8	71 ± 20	NA
All	237 ± 4	124 ± 3	72 ± 3	36 ± 5

Table 12. Occurrence of the half-pounder life history and incidence of repeat spawners among adult steelhead sampled in the lower Klamath River basin in 2007- 2009; including comparisons to data collected in the early 1980's (Hopelain 1998).

River	Years	n	Half-pounder occurrence (%)	Spawning trip (%)			
				1st	2nd	3rd	4th
Klamath	2007-2009	63	96.8	85.7	11.1	3.2	0.0
Trinity	2007-2008	291	11.0	84.5	13.1	2.4	0.0
	1982	45	80.0	68.9	31.1	0.0	0.0
Salmon	2008-2009	11	58.3	63.6	9.1	18.2	9.1
	1981-1983	15	86.7	73.3	26.7	0.0	0.0
Scott	2008	4	75.0	100.0	0.0	0.0	0.0
	1981-1983	78	96.1	73.1	21.8	2.6	2.6
Shasta	2008	8	100.0	87.5	12.5	0.0	0.0
	1981-1983	119	94.1	52.1	29.4	18.5	0.0
All	2007-2009	377	29.2	84.3	12.5	2.9	0.3

2007-2009; yet during a similar study conducted in the early 1980's (e.g., Hopelain 1998), no resident rainbow trout were observed (Hopelain 2010, personal communication). In the Trinity River sub-basin, incidence of the half-pounder life history was lower among fall-run steelhead in 2007 and 2008 than in 1982 (11.0% vs. 80.0%; $\chi^2 = 110.72$, df =1, n=336, $P < 0.001$), and repeat spawners comprised a smaller portion of the catch in 2007 and 2008 than in 1982 (15.2% vs. 31.1%; $\chi^2 = 5.73$, df = 1, n=336, $P = 0.017$). Because sample sizes were limited in the other major tributaries (i.e., Salmon, Scott, and Shasta Rivers), data were pooled in comparisons between current and historic figures for fall-run steelhead from the basin above the Trinity confluence. In this sub-basin, mean incidence of the half-pounder life history did not change between 1981-1983 and 2007-2009 (94.3% vs. 90.4%; χ^2=1.13, df = 1, n= 467, $P = 0.287$); however, repeat spawners made up a larger portion of the adult catch in 1981-1982 than in 2007-2009 (35.8% vs. 16.9%; χ^2=10.28, df = 1, n = 467, $P = 0.001$).

Half-Pounder Maturity

Results suggest that while most half-pounders are immature, both male and female fish are capable of spawning after less than one year at sea. Sex and state of maturity were determined in a total of 100 half-pounders (46 males, 54 females), of which, twelve were classified as mature: eight females and four males. The proportion of mature fish did not differ between the sexes ($\chi^2 = 0.40$, df =1, n = 100, $P = 0.529$). Because these fish were not sampled in a random manner, the proportions are not necessarily representative of the greater population. Gonad weight was greater in mature specimens than in immature specimens (mean ± SE = 18.49 ± 7.23 g vs. 0.31 ± 0.02 g; ANOVA, $F_{1,97} = 49.06$, $P < 0.001$), and this disparity increased over the length of the migration season.

Of the models considered for predicting incidence of maturity in half-pounders, the best fitting model (selected using AIC) included two variables: length at the last freshwater winter, and condition factor at capture (Table 13). Length at the last freshwater winter was greater for mature half-pounders than for immature half-pounders (mean ± SE = 216 ± 10 mm vs. 141 ± 4 mm; ANOVA, $F_{1,96} = 52.96$, $P < 0.001$). Similarly, condition at capture was higher for mature fish than for immature fish (mean ± SE = 1.26 ± 0.04 vs. 1.16 ± 0.02; ANOVA, $F_{1,98} = 4.39$, $P = 0.039$). Immature and mature half-pounders were better distinguished by length preceding ocean entry than by length thereafter, and addition of variables for either smolt age or sex increased the AIC. Because length at the last freshwater winter was a stronger predictor variable than condition factor ($z= 3.06$, $P = 0.002$ vs. $z = 2.35$, $P = 0.019$), and because condition was evaluated several months after formation of the last freshwater annulus, I used a simple logistic regression model to estimate the probability of maturation in half-pounders (Figure 11). This predictive relationship is described by

$$(1) \qquad \Pr[maturation] = \frac{e^{(\alpha+\beta \cdot FLFW)}}{1+e^{(\alpha+\beta \cdot FLFW)}},$$

where FLFW is fork length at the last freshwater winter, $\alpha = -15.0241 \pm 3.6130$ (SE), and $\beta = 0.0727 \pm 0.0185$ (SE).

Table 13. Summary of candidate binary response models for predicting incidence of maturity in half-pounders from the lower Klamath River Basin. Models were ranked according to Akaike's information criterion (AIC), and only the five models with the lowest AIC are shown. Predictor variables included fork length at the last freshwater winter (FLFW), condition factor at capture (COND), smolt age (AGE), and sex (SEX).

Model	AIC	ΔAIC	Significant variables ($\alpha = 0.05$)
FLFW+COND	30.719	0.000	FLFW,COND
FLFW+COND+AGE	32.458	1.739	FLFW,COND
FLFW+COND+SEX	32.771	2.052	FLFW,COND
FLFW+COND+AGE+(COND*AGE)	34.016	3.297	FLFW
FLFW+COND+SEX+(FLFW*SEX)	34.317	3.598	FLFW,COND

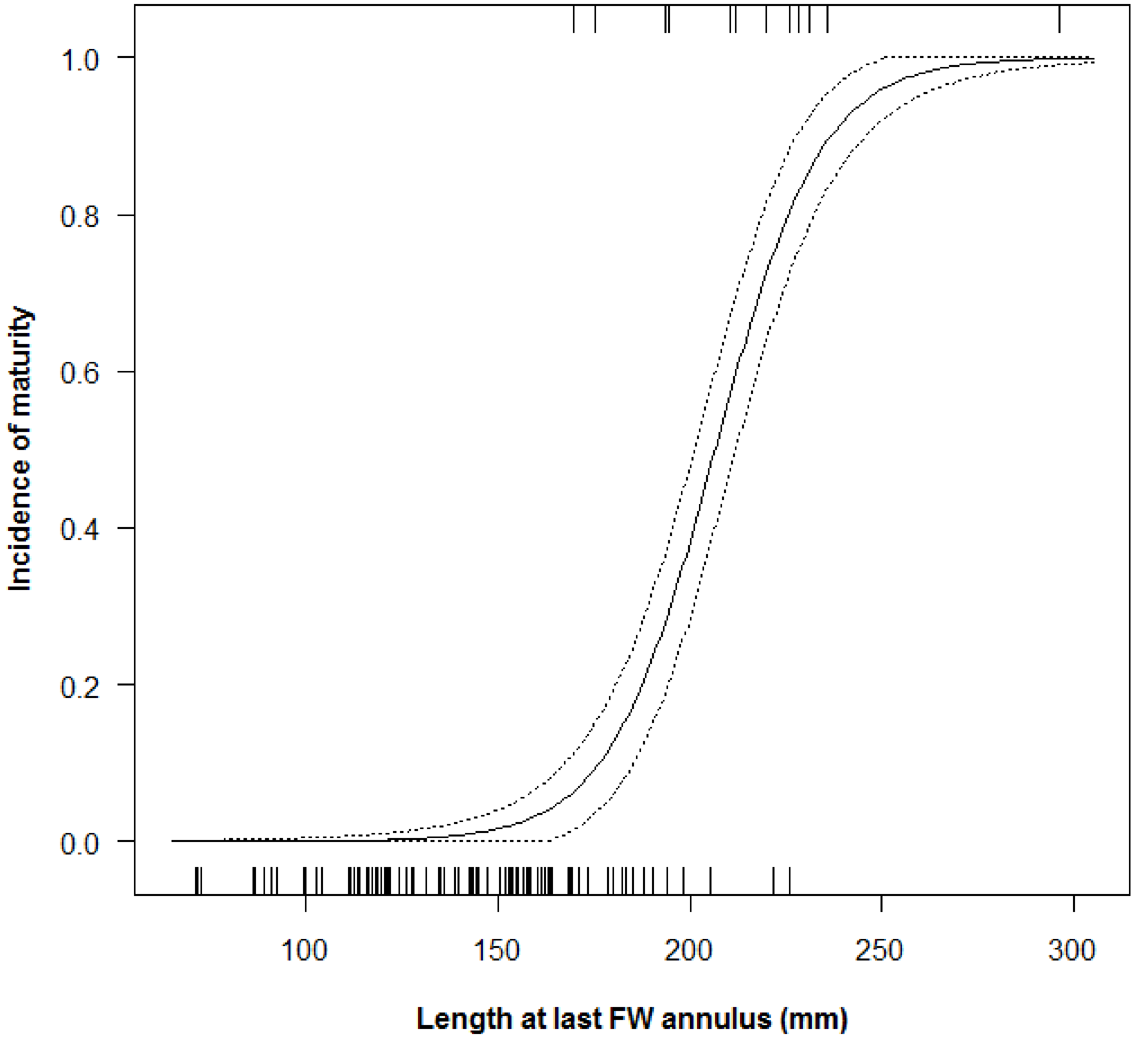

Figure 11. Logistic plot showing observed (tick marks) and predicted (fitted line) incidence of maturity in half-pounders versus fork length in the winter preceding ocean entry. Dashed lines represent a 95% confidence interval on the estimated probability of maturation.

Fecundity

Analysis of fecundity data revealed a positive relationship between fork length and egg number for wild and hatchery steelhead (Figure 12). Fecundity data were collected from 108 hatchery females (fork length: mean ± SE = 624 ± 3 mm; fecundity: mean ± SE = 5008 ± 115 eggs). Total ovarian volume was positively related to fork length ($F_{1,106} = 224.60$, $P < 0.001$, $r^2 = 0.68$). Egg number did not differ between volumetric estimations and hand counts ($t = 0.75$, $df = 9$, $P = 0.475$), confirming the accuracy of this technique. Fecundity was positively and significantly correlated with fork length (FL) in hatchery females ($F_{1,106} = 65.49$, $P < 0.001$, $r^2 = 0.38$), as described by the relationship

$$(2) \qquad \log_e(Fecundity) = \alpha + \beta \cdot \log_e(FL)$$

; where $\alpha = -1.5473 \pm 1.2407$ (SE), and $\beta = 2.4301 \pm 0.3003$ (SE). Data collected from 10 wild fish (fork length: mean ± SE = 494 ± 29 mm; fecundity: mean ± SE = 3249 ± 602 eggs) fell within the bounds of a 95% prediction interval on the fitted hatchery model. Further, the slopes of the individual regression lines for fecundity vs. fork length did not differ between wild and hatchery fish (ANCOVA, $t = -0.14$, $P = 0.888$). Otolith microchemistry revealed that two of the ten mature wild females were resident rainbow trout.

Influencing Factors and Consequences of Life History Trajectories

In general, resident rainbow trout grew faster in freshwater than juvenile steelhead; however, once steelhead were in the ocean, they grew faster than rainbow trout

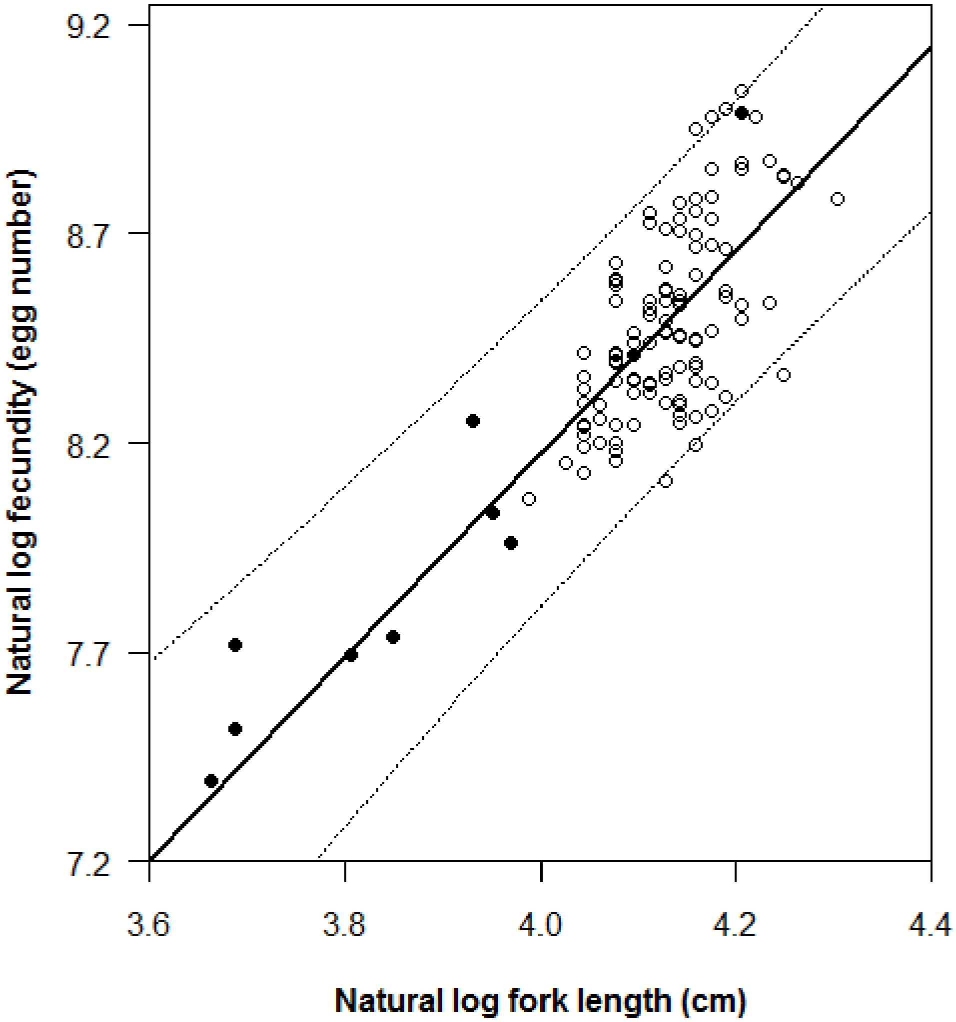

Figure 12. Regression line (solid) and 95% prediction interval (dotted lines) of relationship between fecundity and length in steelhead from Trinity River Hatchery (open circles; $r^2 = 0.38$, $n = 108$). Closed circles represent data collected from 10 wild *Oncorhynchus mykiss* (8 steelhead, 2 rainbow trout) captured in the lower Klamath River Basin.

(Table 14; Figure 13). Comparison between freshwater growth rates for rainbow trout and steelhead highlighted the potential existence of three separate pathways. The fastest growing group of fish smolted at age 1, an intermediate group of fish residualized, and the slowest growing group of fish delayed ocean entry to age 2 or 3. Apparently, conditions affecting growth were less favorable for resident fish than for anadromous fish. Within a year of entering the ocean, steelhead were significantly larger than rainbow trout of equivalent age. Consequently, fecundity in steelhead was greater than fecundity in their nonanadromous counterparts. For example, at age 4, the estimated mean fecundity for rainbow trout was 1,421 ± 161 (SE) eggs, whereas the estimated mean fecundity for steelhead was 4,170 ± 65 (SE) eggs. Of the 23 rainbow trout for which sex could be confidently determined, 10 were male and 13 were female.

Incidence of the half-pounder life history differed notably among sub-basins. For example, the half-pounder phenotype was more prevalent in the Klamath Basin above the Trinity confluence, than in the Trinity River sub-basin alone (91.6% vs. 11.0%; χ^2 = 200.21, df =1, n =375, P < 0.001; Table 12). Neither smolt length (mean ± SE = 204 ± 5 mm vs. 206 ± 2 mm; ANOVA, $F_{1,360}$ = 0.228, P = 0.633) nor sex (51.5% male vs. 44.2% male, χ^2 = 1.25, df = 1, n = 341, P = 0.263) were significantly related to the presence or absence of the half-pounder life history. However, smolt age was lower for steelhead that exhibited the half-pounder trait than for fish that remained in the ocean (mean ± SE = 1.73 ± 0.06 years vs. 1.93 ± 0.03 years; ANOVA, $F_{1,337}$ = 11.93, P < 0.001). Within the Trinity River sub-basin, smolt length was smaller for fish that exhibited the half-pounder life history than for fish that remained in the ocean (mean ± SE = 181 ± 6 mm vs. 206 ± 2

Table 14. Comparison of mean ± SE growth between rainbow trout and steelhead from the lower Klamath River Basin. Gray cells represent comparisons between freshwater and saltwater growth rates. Significant differences (two-sample t-test, α =0.05) in age-specific growth between rainbow trout and steelhead are highlighted in bold (n = 591).

	Growth (mm·year^{-1})			
		Steelhead		
Age interval	Rainbow trout vs.	Smolt age = 1	Smolt age = 2	Smolt age = 3
0-1	106 ± 3	112 ± 2	**90 ± 1**	**86 ± 2**
1-2	103 ± 7	**197 ± 9**	**80 ± 2**	**63 ± 4**
2-3	124 ± 8	**161 ± 7**	**250 ± 5**	**68 ± 5**
3-4	77 ± 11	**80 ± 5**	**114 ± 3**	**235 ± 14**
4-5	58 ± 10	40	67 ± 4	**116 ± 8**

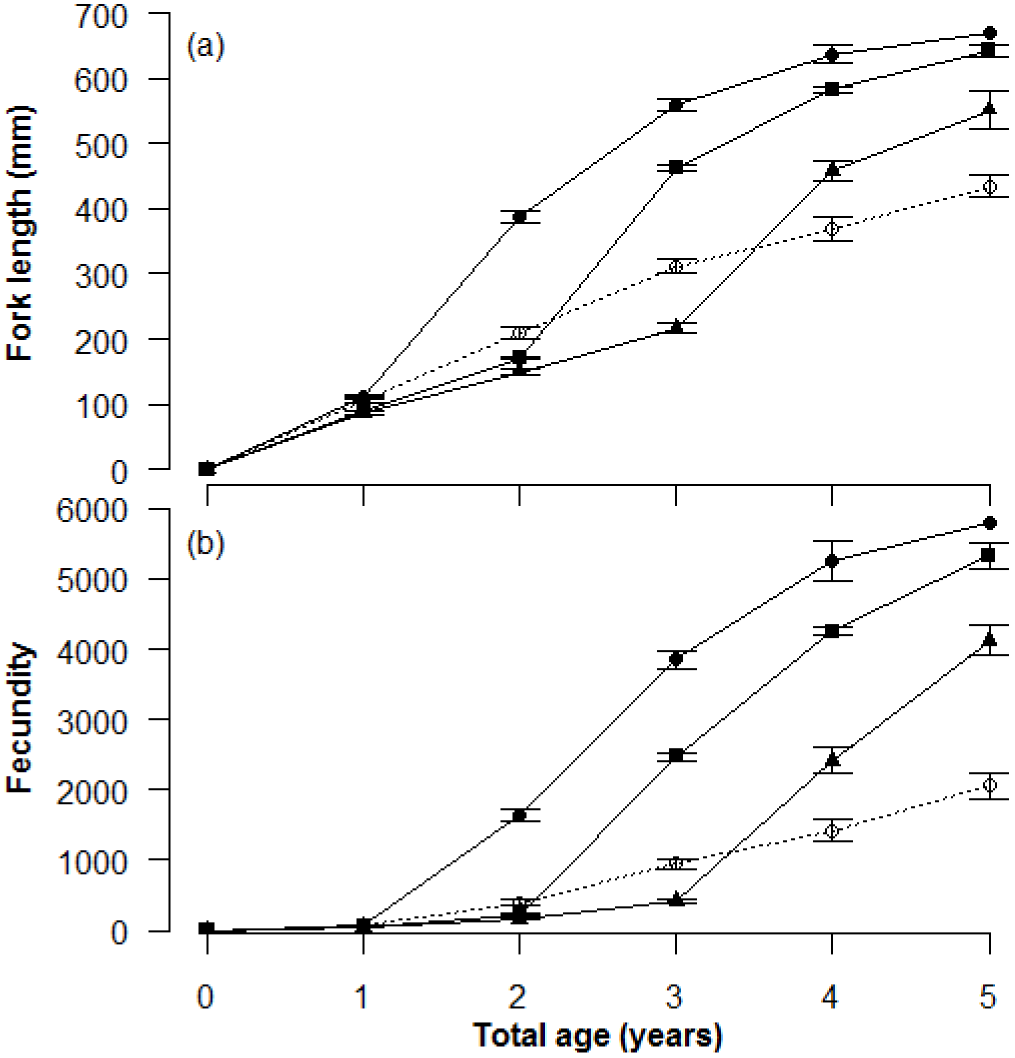

Figure 13. Mean length at age (a) and estimated fecundity (b) for steelhead (solid lines; smolt age: 1 (circles), 2 (squares), and 3 (triangles)) and rainbow trout (dotted line; open circles) from the lower Klamath River Basin. Fecundity was estimated according to the equation Fecundity = $\alpha \cdot FL^{\beta}$; where $\alpha = 0.2128$ (95% confidence limits: 0.0615, 0.7359), and $\beta = 2.4301 \pm 0.3003$. Error bars represent ± 1SE ($n = 591$).

mm; ANOVA, $F_{1,282} = 16.57$, $P < 0.001$). Similarly, smolt age was lower for steelhead that exhibited the half-pounder phenotype than for fish that exhibited the ocean contingent phenotype (mean ± SE = 1.52 ± 0.11 years vs. 1.93 ± 0.03 years; ANOVA, $F_{1,266} = 20.79$, $P < 0.001$). For the rest of the basin, small and unbalanced sample sizes precluded a rigorous comparison between groups, though summary statistics illustrated general trends. In the basin upstream of the Trinity confluence, smolt length was larger for fish that exhibited the half-pounder life history than for fish that remained in the ocean (mean ± SE = 214 ± 6 mm vs. 208 ± 18 mm). In contrast, smolt age was lower for fish that exhibited the half-pounder phenotype than for fish that expressed the ocean contingent phenotype (mean ± SE = 1.82 ± 0.07 years vs. 2.00 ± 0.26 years).

To isolate the consequences of the half-pounder life history, I compared length and growth for three sets of parallel trajectories (1/1.2s vs. 1/h.2s, 2/1.2s vs. 2/h.2s, and 3/1.2s vs. 3/h.2s). Mean growth in the first year at sea was significantly greater for fish that remained in the ocean than for fish that returned to freshwater on a half-pounder migration (Table 15; Figure 14). Consequently, fish expressing the ocean contingent phenotype were significantly larger than fish expressing the half-pounder phenotype at the end of the first and second saltwater winters, and still marginally larger at the end of the third saltwater winter. Following the end of the first saltwater winter, individuals of the half-pounder phenotype grew faster than individuals of the ocean contingent phenotype, indicating some level of compensatory growth. Nonetheless, the extra growth accrued in the first year at sea afforded ocean contingents a fecundity advantage at the first and second spawning events. Using Equation 2, I predicted fecundity at age and

Table 15. Comparison of mean ± SE fork length at life history stages (gray cells) and growth between life history stages (white cells) for parallel life history trajectories (i.e., those that differ only in the presence/absence of a half-pounder migration); and results of two-sample t-tests (OE = ocean entry, SW = saltwater winter; n = 309).

	FL (mm)		
Life history stage	1/1.2s	1/h.2s	**P**
OE	203 ± 6	173 ± 7	0.002
	264 ± 10	167 ± 8	<0.001
1SW	466 ± 9	341 ± 6	<0.001
	126 ± 6	171 ± 10	<0.001
2SW	592 ± 6	512 ± 13	<0.001
	70 ± 8	81 ± 4	0.267
3SW	648 ± 16	587 ± 26	0.086
	2/1.2s	2/h.2s	
OE	207 ± 2	226 ± 7	0.011
	293 ± 3	143 ± 6	<0.001
1SW	501 ± 3	369 ± 6	<0.001
	102 ± 2	141 ± 5	<0.001
2SW	602 ± 3	509 ± 6	<0.001
	52 ± 5	73 ± 7	0.019
3SW	640 ± 9	574 ± 9	<0.001
	3/1.2s	3/h.2s	
OE	214 ± 8	229 ± 16	0.414
	282 ± 13	168 ± 22	0.002
1SW	496 ± 17	398 ± 22	0.004
	107 ± 10	128 ± 16	0.295
2SW	603 ± 13	526 ± 10	<0.001
	NA	51	NA
3SW	NA	615	NA

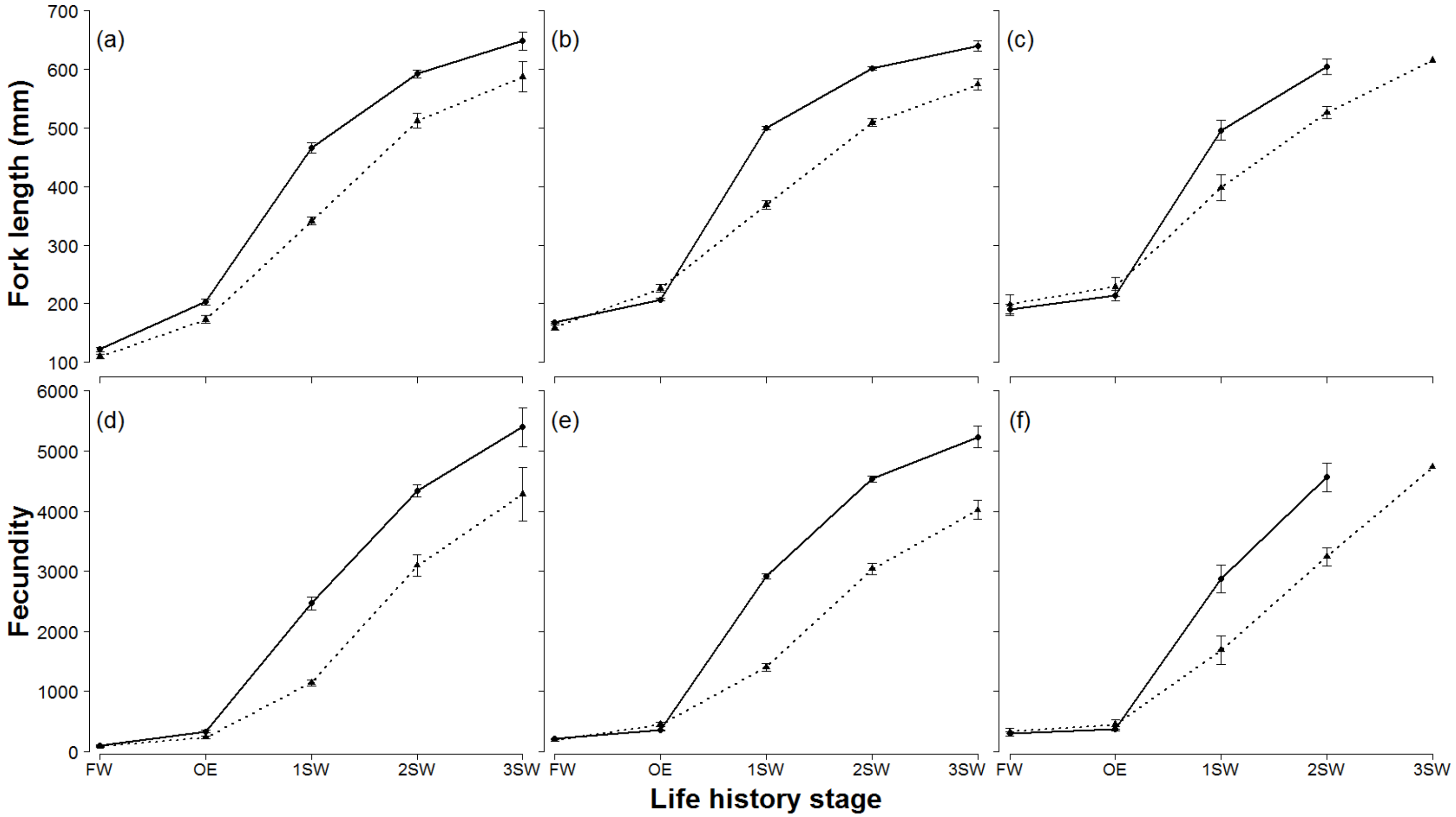

Figure 14. Comparison of observed mean length (a-c) and estimated fecundity (d-f) at last freshwater annulus (FW), ocean entry (OE), and first through third saltwater winters (1-3SW) for fish that did (triangles and dashed lines) and did not (circles with solid line) exhibit the half-pounder life history: (a,d) 1/h.2s vs. 1/1.2s, (b,e) 2/h.2s vs. 2/1.2s, and (c,f) 3/h.2s vs. 3/1.2s. The second and third saltwater winters (2SW and 3SW) represent the first and second spawning migrations, respectively. Fecundity was estimated according to the equation Fecundity = $\alpha \cdot FL^{\beta}$; where $\alpha = 0.2128$ (95% confidence limits: 0.0615, 0.7359), and $\beta = 2.4301 \pm 0.3003$. Error bars represent ± SE (n = 309).

cumulative fecundity for female steelhead in each of the six life history categories (Table 16; Figure 14). The results suggest that female steelhead of the half-pounder phenotype will on average, produce 1,441 ± 93 (SE) fewer eggs at the first spawning event than fish of the ocean contingent phenotype. Further, for second-time spawners, the average cumulative cost of the half-pounder migration is approximately 2,410 ± 409 (SE) eggs.

For a small proportion of half-pounders, the first migration back into freshwater represented a maiden spawning voyage. Using Equation 1, I estimated the probability that a random sample of adult steelhead had reached maturity during a prior half-pounder migration. The results suggest that approximately 7.6% (n = 92) of half-pounders would have been capable of spawning. Of the seven fish (two males, five females) for which the probability of maturation was greater than 50%, four smolted at age 2 and three smolted at age 3.

To further evaluate the consequences of the half-pounder life history, I examined the data to determine if fish exhibiting the trait experience a greater degree of iteroparity than fish that do not. Incidence of the half-pounder life history was higher in second time spawners than in first time spawners (46.8% vs. 26.4%; $\chi^2 = 7.30$, df = 1, n = 365, P = 0.007); and while the differences were insignificant, incidence rates were also higher in third (36.4%, n = 11) and fourth time (100%, n = 1) spawners.

Table 16. Comparison of estimated mean ± SE fecundity for parallel life history trajectories (i.e., those that differ only in the presence/absence of a half-pounder migration) through two spawning events (n = 309). Fecundity was estimated according to the equation: Fecundity = $\alpha \cdot FL^{\beta}$; where $\alpha = 0.2128$ (95% confidence limits: 0.0615, 0.7359), and $\beta = 2.4301 \pm 0.3003$.

	Fecundity		
Life history	1st spawn	2nd spawn	Cumulative
1/1.2s	4,337 ± 105	5,396 ± 324	9,490 ± 609
1/h.2s	3,092 ± 178	4,282 ± 442	7,268 ± 774
Difference	1,245 ± 206	1,114 ± 548	2,222 ± 774
2/1.2s	4,534 ± 53	5,236 ± 176	9,508 ± 346
2/h.2s	3,035 ± 96	4,019 ± 156	6,900 ± 229
Difference	1,499 ± 110	1,217 ± 235	2,608 ± 415
3/1.2s	4,563 ± 235	5,723*	10,286*
3/h.2s	3,242 ± 154	4,733	8,567
Difference	1,321 ± 281	990	1,719
Mean (/1.2s)†	4,510 ± 47	5,286 ± 151	9, 552 ± 294
Mean (/h.2s)†	3,069 ± 80	4,158 ± 167	7,142 ± 284
Mean Difference	1,441 ± 93	1,1128 ± 225	2,410 ± 409

* Value estimated by projecting length to the third saltwater winter (665 mm)

†Weighted by respective proportions of fish smolting at age 1, 2, and 3 (ocean contingent phenotype (0.13, 0.81, 0.06); half-pounder phenotype (0.34, 0.59, 0.07).

DISCUSSION

Among the factors reflected in basin-specific capture histories, method of capture affected both sample size and the size distribution of fish. For example, because half-pounders were numerous in the mainstem, and because these fish continue to feed in freshwater (Kesner and Barnhart 1972), the length-frequency histogram for the Klamath River was dominated by half-pounders. In contrast, because CDFG weirs were size selective, and because the half-pounder runs in the Trinity and Shasta Rivers were comparatively small, most of the fish sampled in those two tributaries were adult steelhead. The large overall sample size in the Trinity River sub-basin reflected both the magnitude of the run, and the reliability of resistance weirs in capturing migratory steelhead. By comparison, capture histories in the Salmon and Scott Rivers reflected the challenge of hook and line sampling on the tributaries.

Results of otolith microchemistry suggest that anadromous and nonanadromous forms of wild *O. mykiss* occur sympatrically in the lower Klamath River Basin. These results coincide with studies documenting co-occurrence of steelhead and rainbow trout outside the basin (e.g., Zimmerman and Reeves 2000; Narum et al. 2004; McMillan et al. 2007). In addition, these findings corroborate evidence from Chesney (2003) and Donohoe et al. (2008) that hatchery *O. mykiss* exhibit both anadromous and resident forms within the basin.

The finding of ocean-rearing in half-pounders does not support Savvaitova's (2005) hypothesis that fish are physiologically obligated to remain in the estuary.

Incidentally, the two half-pounders classified as estuary-rearing may have also entered the ocean, but for a period of time that was imperceptible given the protocol. Because the incorporation period (i.e., amount of time required for the chemical composition of an otolith to match that of the aquatic environment) was unknown, I used statistical principles to guide analysis. For example, in determining migratory history, $^{87}Sr/^{86}Sr$ ratios were integrated over 40 µm because that distance represented one independent sample (i.e., one laser beam diameter).

Determinations of maternal origin suggest that both steelhead and rainbow trout are capable of producing progeny of the alternative life history form. In general, it appeared that the majority of steelhead were of anadromous maternal origin. My findings are consistent with results reported by Zimmerman and Reeves (2000), who observed that most *O. mykiss* from the Babine River in British Columbia exhibited the same life history as their maternal parent; however, the authors observed both anadromous progeny of rainbow trout (1 of 24), and nonanadromous progeny of steelhead (2 of 9). In contrast, Zimmerman and Reeves (2000) observed that all *O. mykiss* from the Deschutes River in Oregon exhibited the same life history as the maternal parent. Similarly, Donohoe et al. (2008) found that all steelhead from Scott Creek in California were progeny of anadromous females. Overall, these studies suggest that the relationship between maternal origin and migratory history may differ among locations.

Determinations of maternal origin should be viewed conservatively for two reasons. First, because freshwater residence prior to spawning can “dilute” the maternal marine influence in progeny of anadromous females (Volk et al. 2000; Donohoe et al.

2008), fish may have been falsely classified as progeny of nonanadromous maternal origin. Previous research shows that in progeny of steelhead with difficult migrations, and in progeny of stream maturing steelhead, the chemical composition of the otolith core may reflect the freshwater environment rather than the marine environment (Volk et al. 2000; Donohoe et al. 2008). As a particularly relevant example, Donohoe et al. (2008) reported limited reliability in using otolith microchemistry (Sr/Ca) to determine maternal origin in *O. mykiss* from Iron Gate and Trinity River Hatcheries. The general explanation was that the sampled fish had faced a relatively difficult migration, and had therefore spent a relatively long time in freshwater before spawning (Donohoe et al. 2008). Since most of the otoliths analyzed in this study came from fall-run (summer) steelhead with potentially comparable migrations, I can't rule out the possibility of a similar dilution effect. Second, because one of the streams within the lower Klamath River Basin could have an $^{87}Sr/^{86}Sr$ ratio that exceeds the global marine value, fish may have been falsely classified as progeny of anadromous maternal origin. For six specimens, the $^{87}Sr/^{86}Sr$ ratio in the freshwater region of the otolith exceeded 0.70918, which suggests either that fish were strays from outside the basin, or that the $^{87}Sr/^{86}Sr$ ratio of a tributary within the basin is higher than the global marine value. Because either a freshwater or marine maternal influence could create a decrease in the $^{87}Sr/^{86}Sr$ ratio around the otolith core for these six fish, maternal origin was recorded as unknown. However, another source of potential error exists. A resident female could conceivably rear in a stream where the $^{87}Sr/^{86}Sr$ ratio is greater than 0.70918, and spawn in a stream where the $^{87}Sr/^{86}Sr$ ratio is less than 0.70918. Consequently, progeny of this female would have an elevated

^{87}Sr/^{86}Sr ratio in the otolith core, giving the false impression of a maternal marine influence.

The finding that *O. mykiss* may give rise to progeny of the alternative life history form suggests that rainbow trout and steelhead may share a common gene pool (Zimmerman and Reeves 2000). Previous work has provided strong evidence of reproductive exchange between steelhead and rainbow trout. For example, Seamons et al. (2004) found genetic evidence that resident males made significant contributions to the steelhead population in Snow Creek, Washington. Similarly, McPhee et al. (2007) used microsatellite DNA to confirm that there was gene flow between alternative life history forms in *O. mykiss* from Kamchatka, Russia. McMillan et al. (2007) observed interbreeding between female steelhead and male residents in the Sol Duc and Calawah basins of Washington. Because I do not have direct, corroborating evidence of genetic exchange between anadromous and nonanadromous forms of *O. mykiss*, results of otolith microchemistry should be interpreted as merely suggestive with respect to interbreeding.

This study's results suggest that scale pattern analysis was a reliable (94-97% accurate) method for determining migratory history in *O. mykiss* from the lower Klamath River Basin. With visual scale analysis, the greatest challenge was in distinguishing between anadromous and nonanadromous fish; specifically, when scale patterns (i.e., circulus increments) were neither distinctly representative of freshwater growth, nor distinctly representative of ocean growth. However, the creation of an objective rule for distinguishing between anadromous and nonanadromous fish helped improve scale analysis. While qualitative scale analysis resulted in one more misclassification of life history form than quantitative scale analysis, visual methods were advantageous in certain situations. For example, in one instance, the naked eye was able to perceive a feature in the scale pattern that was left undetected by quantitative methods. Consequently, life history form was correctly classified by visual methods, but misclassified by the logistic regression model.

Overall, my findings suggest that conventional assumptions regarding circuli spacing were largely (~97%), but not totally, effective in distinguishing between anadromous and nonanadromous fish in the lower Klamath River Basin. Thus, it is suggested that the freshwater growth rate of one fish can potentially exceed the ocean growth rate of another. Since quantitative scale analysis was significantly more time consuming that qualitative scale analysis, while providing no significant improvement to the classification accuracy, visual methods appear to be a reasonable and efficient way to determine migratory history. However, when resources are available, a comparative validation process (i.e., between otoliths and scales) can ultimately improve reader performance.

This study contributes to an existing body of evidence reporting diversity of life history in *O. mykiss* (e.g., Shapovalov and Taft 1954; Busby et al. 1996; Thorpe 1998). For example, my findings suggest that fish from the lower Klamath River Basin may exhibit at least 33 different life history categories at maturity. While there are clearly numerous pathways by which a fish might spawn, all *O. mykiss* in the basin appear to follow one of three basic trajectories: nonanadromous, anadromous with a half-pounder migration, and anadromous without a half-pounder migration. Previous work suggests that expression of life history in *O. mykiss* is determined by a combination of environmental (McPhee et al. 2007), and perhaps to a lesser degree, genetic factors (Tipping 1991; Martyniuk et al. 2003; Thrower et al. 2004). Thus, which of the three basic trajectories a fish from the Klamath River follows, depends largely upon the conditions of the local environment.

This study's results regarding freshwater age and growth are generally consistent with expected values for *O. mykiss* in the region. For example, Busby et al. (1996) reported that for steelhead in California, the average proportions of age 1, 2, 3, and 4 smolts are 23.3%, 69.0%, 7.5%, and 0.3% respectively. In productive waters, rainbow trout are expected to reach lengths of 140-150 mm FL in one year, reach lengths of 380-400 mm FL in four years, and grow 30-50 mm FL in each subsequent year (Snider and Linden 1981, as cited by Moyle 2002). In comparison, juvenile steelhead might reach 100-120 mm FL in one year, reach 160-170 mm FL in two years (Moyle 2002), and enter the ocean at a length of 100-250 mm FL (Hopelain 1998).

The finding of a negative relationship between smolt age and growth is consistent with patterns observed in *O. mykiss*, and similarly consistent with patterns observed among the salmonids. For example, Peven et al. (2004) observed a negative relationship between freshwater growth and smolt age in steelhead from the mid-Columbia River Basin, Washington. Similarly, Thériault and Dodson (2003) observed a negative relationship between freshwater growth and smolt age in brook char (*Salvelinus fontinalis*) from the Sainte-Marguerite River, Quebec Province, Canada. Hutchings and Jones (1998) reported that a negative relationship between freshwater growth and smolt age is typical of Atlantic salmon (*Salmo salar*) throughout their distribution. Likewise, *O. mykiss* from higher latitudes and presumably less productive streams typically smolt at older ages than fish from lower latitudes and presumably more productive streams (Busby et al. 1996; Satterthwaite et al. 2009).

My findings regarding half-pounders coincide with the literature on some points, yet contrast with the literature on others. For example, my observations were consistent with those of Everest (1973) on several points. First, Everest (1973) reported that most half-pounders re-entered the Rogue River in August and September, and remain in freshwater for an average of six months. Second, Everest (1973) noted that half-pounders grew an average of 119 mm between the time of ocean entry and freshwater re-entry. Third, Everest (1973) reported that the mean length at capture for half-pounders was 356 mm FL. In contrast, I observed a greater range in length at capture for half-pounders than was previously reported in the lower Klamath River Basin; primarily because I used salt age (i.e., one year at sea) to define the life history, whereas others (e.g., Kesner and Barnhart 1972; Hopelain 1998) projected size criteria onto salt age to define the life history. Interestingly, if the fish from these prior studies are re-categorized, then the results are more consistent with those of the present study. For example, if Kesner and Barnhart (1972) had categorized half-pounders solely by salt age, rather than in part by size (250-349 mm), then the authors would have reported that half-pounders reach lengths of almost 500 mm (Quinn and Myers 2004). Incidentally, the term half-pounder is a misnomer in the literal sense, as my results suggest that the mean weight at capture was closer to one pound than to half of one pound. Semantics aside, the defining criteria for half-pounders are nonetheless inconsistent within the literature (Busby et al. 1994). A need exists for an objective and universal definition by which managers and researchers can define the half-pounder. I would argue that the criteria adopted in this study represent the appropriate choice.

This study's results regarding ocean age and ocean growth of steelhead revealed both similarities and differences relative to the expected range of values. Results for sea age at first maturity were generally consistent with regional observations. For example, in their review of West Coast steelhead, Busby et al. (1996) reported that most steelhead spawn after spending two years at sea. Results for ocean growth show instances of both consistent and contradictory results. On one hand, the aforementioned similarity in growth for Rogue and Klamath River half-pounders at sea suggests that ocean growth rates are comparable between stocks. On the other hand, comparison between length at age data presents the possibility that Klamath steelhead have reduced ocean growth rates relative to other stocks. For example, Shapovalov and Taft (1954) reported that the mean lengths of maiden spawners in the age categories 1/2, 2/2, and 3/2 (equivalent to 1/1.1s, 2/1.1s, and 3/1.1s) were 651 mm, 680 mm, and 695 mm, respectively. While it appears that steelhead from Waddell Creek are significantly larger at age than steelhead from the Klamath, the results of such a comparison cannot be considered conclusive given the vast differences in time and space.

This study's findings regarding incidence of the half-pounder trait and incidence of repeat spawners coincide with prior results for the basin, and for the region. For example, Hopelain (1998) reported that the frequency of the half-pounder life history ranged from 17.8 to 100.0% in the lower Klamath River basin, while the frequency of first-time spawners ranged from 36.4 to 82.3% in the lower Klamath River basin. Because some half-pounders are capable of spawning, incidence of iteroparity was likely underestimated in both studies; however, the negative bias was presumably similar between studies. Despite the variation among sub-basins, the reproductive histories observed in the lower Klamath River Basin are generally consistent with expected regional values. For example, Busby et al. (1996) reported that on average, 81.5% and 85.0% of adult steelhead in California and Oregon are maiden spawners, respectively. Shapovalov and Taft (1954) found that 82.8% of adults were first-time spawners, 15.0% of adults were second-time spawners, 2.1% of adults were third-time spawners, and less than 1% of adults were fourth-time spawners. My finding of an unbalanced sex ratio in repeat spawners is consistent with a large number of studies reporting greater iteroparity in female steelhead than in male steelhead (e.g., Busby et al. 1996; Evans et al. 2004; Keefer et al. 2008).

While the observed temporal changes, or lack thereof, in life history structure suggest that the conditions favoring certain pathways are variable, conclusions should be drawn with caution. Of particular interest was the observed change in incidence of the half-pounder life history in the Trinity River between 1981 and 2007. That the frequency of occurrence declined significantly in this sub-basin alone suggests that Trinity stocks have experienced environmental alteration resulting in either phenotypic plasticity or genetic change. However, because neither my samples nor those of Hopelain (1998) were necessarily representative of the greater population, particularly when sample sizes were low, changes in rates of incidence should be interpreted conservatively.

The finding that length-at-age influenced incidence of maturity in half-pounders is consistent with studies reporting a positive relationship between size and precocious maturation in salmonids. For example, Kesner and Barnhart (1972) observed that among steelhead returning in the year of initial ocean entry, mature fish tended to be greater than 349 mm FL. Everest (1973) observed that among half-pounders from the Rogue River, the sexually mature specimens were generally the largest (> 380 mm FL) and fastest growing fish within the cohort. In an experiment with coho salmon, Appleby et al. (2003) demonstrated that the frequency of jacks within a cohort could be increased by increasing smolt size. I expect that incidence of sexual maturity in half-pounders may similarly increase with improved freshwater productivity. That fork length at the last freshwater annulus was a better predictor of maturation than fork length at ocean entry suggests that an individual steelhead's physiological trajectory is determined in freshwater, prior to ocean entry and exposure to conditions in the marine environment. This suggestion is consistent with the findings of Vøllstad et al. (2004), who reported that size prior to ocean entry had a significant influence on the tendency for jacking in both coho and Chinook salmon.

My finding that both male and female steelhead can spawn in the year of initial ocean entry contrasts with conventional wisdom regarding precocious maturation in the species of *Oncorhynchus* (e.g., Willson 1997; Moyle 2002; Quinn 2005). Among the literature, evidence of precocious maturation in female steelhead is scarce. Of the two citations I was able to locate, both pertained directly to half-pounders. Kesner and Barnhart (1972) observed that among steelhead returning to the Klamath River in the year of initial ocean entry (i.e., half-pounders by my definition; n = 202), there were equal numbers of sexually mature males and females (6 males, 6 females). Savvaitova et al. (2005) reported that among the Kamchatka (Russia) half-pounders that were classified as sexually mature (19 of 189), only one was female. In contrast, Everest (1973) observed that none of the sexually mature half-pounders (3 of 84) captured in the Rogue River were female. The unnaturally high incidence of precocious maturation in female steelhead from the lower Klamath River Basin could reflect one of two possible scenarios. Observed rates of incidence may in fact reflect a situation that is more geographically common than we know. Alternatively, because of unique genetic or environmental qualities, early maturation may be more heavily favored in Klamath stocks than in stocks elsewhere.

This study adds to existing evidence of the positive relationship between female size and reproductive output (i.e., fecundity and egg size) in salmonids (e.g., Quinn and Bloomberg 1992; Jonsson and Jonsson 1999; Einum et al. 2003). For the length-fecundity regression model, the slope that I derived empirically (b = 2.430) fell within the bounds of previously observed values for *O. mykiss*. For example, Shapovalov and Taft (1954) calculated a slope of 2.117, and Ward and Slaney (1993) calculated a slope of 3.053. My findings that egg number explained only 68% of the variation in total ovarian volume, and that fork length was negatively correlated with the number of eggs per unit volume, suggest that reproductive output varied as a function of both egg number and egg size. Hence, that fork length explained more of the variation in total ovarian volume than variation in egg number, could be explained by a trade-off between egg number and egg size (Beacham and Murray 1993; Quinn et al. 1995). That is, while total reproductive effort increased with body size, finite energy resources were split between the production of more eggs and the production of larger eggs.

Results of this study suggest that natal origin (i.e., sub-basin) and growth influence whether or not fish exhibit an anadromous or nonanadromous life history; and to some degree, the apparent effect of the former may be a function of the latter. The observed sub-basin effect may be explained in a number of ways. First, the tendency for anadromy (residency) may decrease (increase) with increasing migratory difficulty (Kristoffersen 1994; Wood 1995). Evidence to support this notion, albeit anecdotal, is provided by a comparison between capture histories for the Salmon (rkm 106) and Scott Rivers (rkm 230). However, the relationship between migratory difficulty and residency was confounded to some degree by method of capture. For example, I expect that my spatially stratified hook and line sampling regime was more effective in capturing resident fish than were the weirs, which had a fixed location of capture. Evidence to support this notion is provided by a comparison between capture histories from the Shasta (rkm 285) and Salmon Rivers (rkm 106). Second, the tendency for residency or anadromy may be under some genetic control (Thrower et al. 2004). Because there is evidence of genetic distinction among locations in the lower Klamath River Basin (Pearse et al. 2007), fish from one tributary may be more or less pre-disposed to residency than fish from another tributary. Third, the tendency for residency or anadromy may be a function of environment; thus, a function of productivity and growth. My finding that growth (or size at age) influences the likelihood that fish adopt a resident life history is consistent with a number of studies regarding partially migratory salmonids (e.g., Krogius 1982; Strand and Heggberget 1994; Thériault and Dodson 2003). For example, Krogius (1982) reported that the incidence of residency in sockeye salmon (*O. nerka*) was positively related to density-dependent growth. Thériault and Dodson (2003) reported that among age-1 brook char, smaller fish delayed smoltification, whereas larger fish either outmigrated or residualized. However, contrary to my findings, Thériault and Dodson (2003) observed that for the larger age-1 brook char, outmigrants and residents did not differ in size.

Results of my study extend observations (e.g., Gross 1987; Hutchings and Morris 1985) that nonanadromous individuals are smaller at age, and consequently less fecund (Shapovalov and Taft 1954; Ward and Slaney 1993) than anadromous individuals. Gross (1987) noted that on average, anadromous salmonid phenotypes are three times as fecund as their resident counterparts. While an apparent cost of residency is reduced age-specific reproductive output, a resident life history may confer certain benefits. For example, survivorship is expected to be greater in nonanadromous forms than in anadromous forms (Gross 1987; Quinn 2005; Hendry et al. 2004). In addition, resident rainbow trout are more likely to spawn repeatedly than are steelhead (Fleming 1998; Quinn 2005). Overall, that some *O. mykiss* in the basin reside in freshwater for the duration of their lives suggests that conditions exist under which a resident life history is favored (Gross 1987; Hendry et al. 2004).

My observation of more female residents than male residents contrasts with numerous studies regarding partially migratory salmonids (e.g., Krogius 1982; Jonsson and Jonsson 1993; Hutchings and Jones 1998). For example, Jonsson et al. (2001) observed that within a population of brown trout (*Salmo trutta*), 3.7% of the adults were resident females, whereas 48.9% of the adults were resident males. Hutchings (1986) reported a similar preponderance of males in resident Atlantic salmon. Because increased size is generally expected to provide a greater fitness benefit to female salmonids than to male salmonids, the tendency for residency is expected to be greater in males (Hendry et al. 2004).

Results suggest that sub-basin of natal origin and smolt age influence the likelihood that fish will exhibit the half-pounder life history. The degree to which each of these effects may be a product of genetic versus environmental factors, or a product of the two, is unknown (Busby et al. 1994). An informal breeding experiment suggests that both genetic and environmental components influence occurrence of the half-pounder life history: by selecting against the half-pounder phenotype, managers at the Cole Rivers Hatchery (Rogue River) were able to create a broodstock in which incidence of the life history was relatively low (Evenson (personal communication) as cited by Busby et al. 1994). However, Cramer et al. (1985) noted that subsequent increases in the frequency of the half-pounder life history coincided with increases in hatchery growth rates. My findings regarding the relationship between incidence of the half-pounder life history and freshwater productivity are generally consistent with the findings of Cramer et al. (1985). For example, among sub-basins, fish in the Trinity River exhibited both the smallest length at ocean entry and the lowest incidence of the half-pounder life history; whereas fish in the Shasta River exhibited both the greatest length at ocean entry and the highest incidence of the half-pounder life history. However, Hopelain's (1998) results revealed no such trend. My finding that smolt age is lower in fish that exhibit the half-pounder trait than in fish that do not coincides with the findings of Cramer et al. (1985). Because freshwater growth was generally negatively related to age at ocean entry, it was not surprising that the half-pounder and ocean cohort phenotypes differed in smolt age, but not in smolt length. This result suggests that fish of the half-pounder phenotype grew faster in freshwater than fish of the ocean contingent phenotype, a notion that is also supported by the observation of compensatory ocean growth. However, that the relationship between smolt length and incidence of the half-pounder life history differed between the Trinity River sub-basin, and the basin upstream of the Trinity confluence, suggests that the relationship between growth and expression of life history may be more complex than the results reveal. Further, the imbalance among sub-basins with respect to both incidence of the half-pounder trait and sample size, increases the difficulty of determining where statistical differences between phenotypes might reflect the biological differences controlling the expression of life history.

To further determine what factors influence expression of the half-pounder life history, future studies should ideally work with large sample sizes from multiple sub-basins, over multiple year classes. However, given that adult fish handling facilities are only operated on the Trinity and Shasta Rivers, and that less than 25 steelhead were captured on the Shasta River in 2008, accruing adequate sample sizes of each phenotype across the basin may be challenging. Alternatively, the role of genetic and environmental components in expression of the half-pounder trait might be evaluated through a captive breeding experiment; where fish from several different stocks are raised under varying levels of productivity, and monitored through at least their first year at sea. Because lifetime survival of first-time spawners might be on the order of 0.023% (Shapovalov and Taft 1954), with smolt-to-adult survival as low as 3.5% (Ward 2000), this type of experiment would require large initial sample sizes for meaningful comparisons.

A key result from this study was the identification of both costs and benefits of expressing the half-pounder phenotype. For example, costs of the half-pounder migration are that fish are smaller and less fecund at their first and second spawning episodes, relative to fish that remain in the ocean during their first year at sea. An apparent benefit of the life history, at least for a small proportion of half-pounders, is the opportunity to spawn. In addition, fish that exhibit the half-pounder phenotype may exhibit a greater degree of iteroparity than fish that exhibit the ocean contingent phenotype. However, this latter suggestion should be interpreted cautiously as the observed trend in iteroparity could also simply reflect a difference in rates of incidence (of the half-pounder life history) among cohorts.

Because lifetime fitness is the product of survival and breeding success (Gross 1987), because few half-pounders spawn, and because results showed a fecundity-related fitness cost to the half-pounder migration, benefits of this life history are likely to manifest in survival and the consequences of additional spawning opportunities. To explore this notion, I used Gross’s (1987) approach to lifetime fitness. Since the fitness consequences of migration are best evaluated by considering one life history relative to another (Hendry et al. 2004), I compared the three sets of parallel life history trajectories through two breeding events. Because the fitness value of a tactic is typically estimated as the average value for individuals expressing the trait (Sober 2001), it seemed reasonable to use average fecundity as a proxy for breeding success in each phenotype. First, I estimated the relative fitness of the half-pounder life history under the condition that survivorship from the first to the second breeding events was greater for the half-pounder phenotype than for the ocean contingent phenotype, as was suggested by representation of the half-pounder life history in first and second-time spawners. More specifically, I assumed that survivorship to the first spawning event was equal between parallel life histories (estimated at 0.023%, Shapovalov and Taft 1954), and I assumed that survivorship from the first to the second spawning events was 10.7% (25 of 234) and 26.3% (22 of 84) for the ocean contingent and half-pounder phenotypes, respectively. Next, for a point of comparison, I estimated the relative fitness of the half-pounder phenotype under the condition of optimality; whereby, lifetime survivorship was equal between parallel life histories at 100%. To evaluate the sensitivity of relative fitness estimates to survival parameter estimates, I simulated results while allowing for variation in the nominal probabilities of survival.

Results of the first exercise indicate that if the estimated probabilities of survival were realized, then the average fitness of the half-pounder phenotype through two spawning events would be approximately 192% that of the ocean contingent phenotype (Appendix B). Results of sensitivity analysis indicate that the parameter for survivorship to the first breeding event had a negligible effect on relative fitness estimates. For example, if the probabilities of survival from the first to the second spawning events were fixed, changing the probability of survival to the first spawning event by an order of magnitude (i.e., from 0.023 to 0.23%) only changed the estimate of relative fitness by approximately 2% (i.e., from 192 to 190%). By comparison, survivorship from the first to the second breeding events had a strong effect on relative fitness estimates (Appendix C). Because increased body size may enhance female breeding success by improving more than just egg number and egg size (see Hendry et al. 2004), the relative fitness of the half-pounder phenotype may have been overestimated. Further, because repeat spawners may realize greater individual fitness during their second spawning event than during their first (Seamons and Quinn 2009), the positive fitness effects of iteroparity may have been underestimated. However, since the estimated rates of repeat spawning were based on a calculation using two separate cohorts rather than by tracking one cohort through time, the results should be interpreted conservatively.

Results of the second exercise indicate that if survivorship was equivalent between alternate life histories at 100%, then the lifetime fitness of the half-pounder phenotype would be approximately 74% that of the ocean contingent phenotype (Appendix D). Sensitivity analysis revealed that the value of the survival parameters had a minimal effect on relative fitness estimates (Appendix E). In accordance with conditional strategy theory, an “inferior” phenotype (i.e., one with lower average fitness than another) can be maintained in a population through inheritance in the conditional strategy (Gross and Repka 1998); however, underlying this theory is the assumption that individuals will adopt the tactic that maximizes their fitness, given individual state (i.e., age or size) and tactic frequency (Gross 1996). Thus, it follows that even if the half-pounder phenotype has lower average fitness than the ocean contingent phenotype, the half-pounder migration should nonetheless confer some individual fitness advantage to fish that exhibit the trait. Plainly stated, results of this second exercise suggest that the half-pounder life history exists because fecundity-related fitness costs of migration are, at least on occasion, offset by survival-related fitness benefits. Results of the first exercise illustrate one way in which this might occur.

While the conceptual link between survivorship and fitness is apparent, what remains unexplained is how a fish's amphidromous migration during the first ocean winter would manifest into increased survivorship between the second and subsequent ocean winters. Another, perhaps more intuitive, explanation for existence of a half-pounder life history is that the incursion into freshwater increases the probability that an individual will survive to the first and subsequent breeding events. This suggestion is consistent with the theory presented by Sattherthwaite (1988), who noted that in the results of McPherson and Cramer (1982), smolt-to adult survival was greater in summer steelhead (2.8%), which exhibited a high incidence of the half-pounder life history (~100%), than in winter steelhead (< 1%), which exhibited a low incidence of the half-pounder life history (21%). However, because summer and winter steelhead re-enter freshwater at different times of the year, it's difficult to unequivocally identify the exact time period or rearing habitat in which differential survival may have occurred. To formally test the survival hypothesis, a mark-recapture study might be used to track one or more cohorts from the smolt through adult phases; however, it will be important that fish come from one reproductive ecotype (i.e., all stream-maturing steelhead) so that any differences in ocean-rearing are due solely to the presence or absence of a half-pounder migration.

In summary, my findings suggest that the continued expression of the half-pounder phenotype is favored by precocious maturation and enhanced survival relative to the ocean contingent phenotype. Because the existence of the life history is a function of selective forces and environment, I surmise that the value of the trait will vary in response to the relative costs and benefits of migration. For example, strong ocean upwelling and high marine survival may decrease the relative fitness of the half-pounder phenotype; whereas, poor conditions in the ocean concurrent with favorable conditions inland, may increase the relative fitness of the half-pounder phenotype. Given this line of thinking, it’s interesting to reconsider the relatively low incidence of the half-pounder life history in the Trinity River sub-basin. If steelhead from throughout the lower Klamath River basin experience similar ocean conditions, then the aberrantly low incidence of the half-pounder phenotype in Trinity stocks must be a function of inland conditions: either prior to ocean entry, or during the half-pounder migration. Further, the observed decline in incidence of the half-pounder phenotype between 1982 and 2007, must be a function of changes in these inland conditions.

Results of this study have important implications beyond my suggestions for future research. First, the ability of rainbow trout to give rise to steelhead has important management implications for the Klamath River Basin, where the largest and most complex dam removal project to date is scheduled to begin as early as 2020 (Boxall 2009). When the four major impoundments are removed, the resident population that has been isolated in the upper basin since the early 1900's will once again have access to the ocean (NOAA 2009). Previous work by Thrower et al. (2004) suggests that the potential for anadromy can be retained through generations of residency. If resident rainbow trout can produce anadromous offspring, then fish in the upper basin may contribute towards the recovery of steelhead in the Klamath River Basin as a whole. Given this possibility, it may be prudent to manage *O. mykiss* from the upper and lower basins under a joint conservation strategy. Second, the multitude of life history patterns expressed by *O. mykiss* from the lower Klamath River basin probably has some adaptive significance. For example, that steelhead from the basin exhibit a rare, albeit geographically unique, life history suggests that fish encounter a suite of freshwater and marine conditions that vary in some important way from conditions elsewhere. From a theoretical standpoint (e.g., Hendry et al. 2004), it makes sense that fish would adopt tactics that reduce the costs associated with these conditions, and it's this phenotypic plasticity of *O. mykiss* which allows the species to persist in the face of environmental adversity (Moyle 2002; Moyle et al. 2008). While further information is required before we can reliably predict how *O. mykiss* life history structure might respond to environmental change, my findings do provide managers with some insight into how stage-specific conditions (i.e., freshwater growth) influence life history pathways.

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PERSONAL COMMUNICATION

Hopelain, J. 2010. Retired from California Department of Fish and Game. Personal Communication. 1225 Lincoln Way, Auburn, CA 95603.

Sinnen, W. 2009. California Department of Fish and Game: Trinity River Project. Personal Communication. 5341 Ericson Way, Arcata, CA 95521.

Appendix A. Summary of life history categories observed in *Oncorhynchus mykiss* from the lower Klamath River Basin. Life history was reported according to the notation system presented by Hopelain (1998). A backward slash (/) separates years in freshwater (left) from years in saltwater (right), and a period (.) separates growing years from spawning years. A lowercase *h* denotes a half-pounder run, and a lowercase *s* denotes a spawning run. For fish captured in fall or early winter, the reported age includes the subsequent winter annulus. Sample sizes presented in parenthesis.

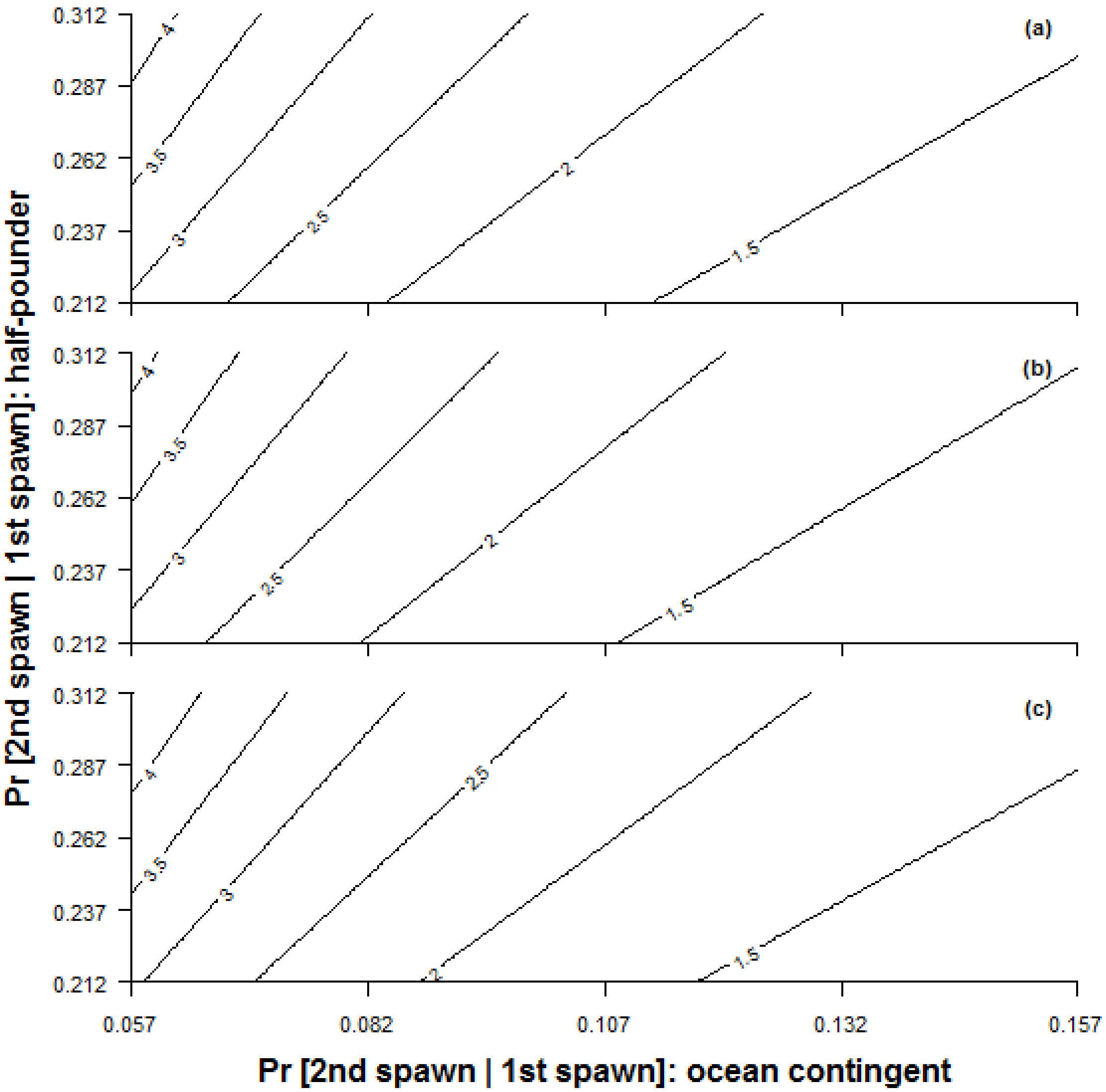
River	Life history categories
Klamath	3/ (9), 4/ (7), 5/ (2); 1/h (29), 2/h (103), 3/h (23); 1/h.1s (14), 1/h.1.1s (1), 2/h.1s (27), 2/1.1s (2), 2/h.2s (3), 2/h.3s (1), 3/h.1s (4), 3/h.2s (1)
Trinity	2/ (1) , 3/ (2), 4/ (1); 1/h (2), 2/h (12), 3/h (4); 1/h.1s (2), 1/h.1.1s (7), 1/h.2s (5), 1/1.1s (24), 1/1.2s (5), 1/2.1s (2), 2/h.1s (3), 2/h.2s (6), 2/h.3s (1), 2/h.1.1s (3), 2/h.1.2s (1), 2/1.1s (168), 2/1.2s (15), 2/1.3s (4), 2/2.1s (11), 2/2.2s (2), 3/h.1s (1), 3/1.1s (12), 3/1.3s (2), 3/2.1s (1)
Salmon	3/ (3), 4/(2), 5/(2), 6/ (1); 1/h (2), 2/h (14), 3/h (1); 1/h.3s (1), 1/h.2.1s (1), 1/h.1.4s (1), 2/h.1s (3), 2/1.1s (1), 2/h.1.1s (1), 2/1.2s (1), 2/1.3s (1), 3/1.1s (1)
Scott	3/ (9), 4/ (1), 5/ (2); 2/h (3); 1/1.1s (1), 2/h.1s (3)
Shasta	4/ (1); 2/h (6), 3/h (3); 1/h.1s (1), 2/h.1s (5), 2/h.2s (1)

Appendix B. Estimated lifetime fitness of the half-pounder phenotype (*hp*) relative to lifetime fitness of the ocean contingent phenotype (*oc*) under the conditions that i) survivorship to the first breeding event (estimated at 0.023%; Shapovalov and Taft 1954) is equal between parallel life history trajectories (1/h.2s vs. 1/1.2s, 2/h.2s vs. 2/1.2s, and 3/h.2s vs. 3/1.2s); ii) survivorship from the first to the second spawning events is 10.7% and 26.2% for the ocean contingent and half-pounder phenotypes, respectively; and iii) breeding success is proportional to fecundity (= $0.2128 \cdot FL^{2.4301}$). Lifetime fitness was calculated following the methods of Gross (1987); whereby the fitness (*W*) realized at a spawning event is the product of survival and breeding success at that spawning event, and lifetime fitness is the sum of the contributions from each of the spawning events.

		1st spawning event		2nd spawning event			
Smolt age	Life history	Survival	Fecundity	Survival*	Fecundity	Lifetime fitness (*W*)	Relative lifetime fitness ($W_{hp} \cdot W_{oc}^{-1}$)
1	1/1.2s	0.00023	4337	0.107	5396	(0.00023·4337) + (0.107·5396)	
	1/h.2s	0.00023	3092	0.262	4282	(0.00023·3092) + (0.262·4282)	1.941
2	2/1.2s	0.00023	4534	0.107	5236	(0.00023·4534) + (0.107·5236)	
	2/h.2s	0.00023	3035	0.262	4019	(0.00023·3035) + (0.262·4019)	1.877
3	3/1.2s	0.00023	4563	0.107	5723	(0.00023·4563) + (0.107·5723)	
	3/h.2s	0.00023	3242	0.262	4733	(0.00023·3242) + (0.262·4733)	2.023
All							**1.924†**

*Survivorship was estimated as the number of second-time spawners displaying a particular phenotype, divided by the number of first-time spawners displaying that same phenotype (ocean contingent: 25 of 234; half-pounder: 22 of 84).

†Weighted by respective proportions of fish smolting at age 1, 2, and 3 (ocean contingent phenotype: 0.13, 0.81, 0.06; half-pounder phenotype: 0.34, 0.59, 0.07).

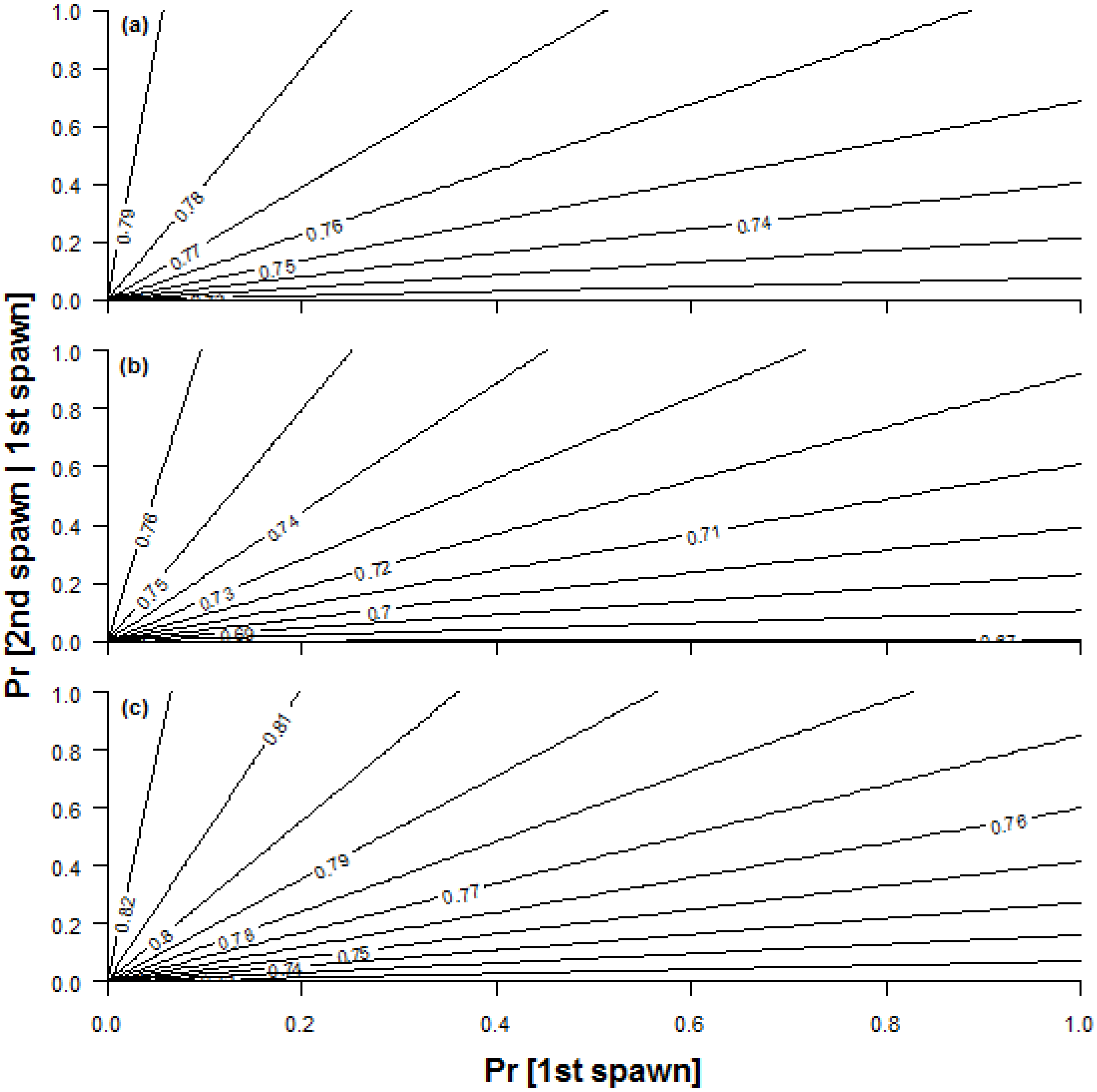


Appendix C. Results of sensitivity analysis for calculations in Appendix B: (a) 1/h.2s vs. 1/1.2s, (b) 2/h.2s vs. 2/1.2s, (c) 3/h.2s vs. 3/1.2s. Isopleths represent the relative lifetime fitness of the half-pounder life history ($W_{hp}\cdot W_{oc}^{-1}$) as a function of survivorship from the first to the second spawning events (Pr[2nd spawn | 1st spawn]) for the ocean contingent (0.107 ± 0.050) and half-pounder pounder phenotypes (0.262 ± 0.050).

Appendix D. Estimated lifetime fitness of the half-pounder phenotype (*hp*) relative to estimated lifetime fitness of the ocean contingent phenotype (*oc*) under the conditions that i) lifetime survivorship is equal between parallel life history trajectories (1/h.2s vs. 1/1.2s, 2/h.2s vs. 2/1.2s, and 3/h.2s vs. 3/1.2s) at 100%, and ii) breeding success is proportional to fecundity (= $0.2128 \cdot FL^{2.4301}$). Lifetime fitness was calculated following the methods of Gross (1987); whereby the fitness (*W*) realized at a spawning event is the product of survival and breeding success at that spawning event, and lifetime fitness is the sum of the contributions from each of the spawning events. A constant (*s*) denotes the probability that a fish of smolt age *i* (1-3) will reach spawning event *j* (1-2).

		1st spawning event		2nd spawning event			
Smolt age	Life history	Survival	Fecundity	Survival	Fecundity	Lifetime fitness (*W*)	Relative lifetime fitness ($W_{hp} \cdot W_{oc}^{-1}$)
1	1/1.2s	s_{11}	4337	s_{12}	5396	$4337 \cdot s_{11} + 5396 \cdot s_{12}$	
	1/h.2s	s_{11}	3092	s_{12}	4282	$3092 \cdot s_{11} + 4282 \cdot s_{12}$	0.758
2	2/1.2s	s_{21}	4534	s_{22}	5236	$4534 \cdot s_{21} + 5236 \cdot s_{22}$	
	2/h.2s	s_{21}	3035	s_{22}	4019	$3035 \cdot s_{21} + 4019 \cdot s_{22}$	0.722
3	3/1.2s	s_{31}	4563	s_{32}	5723	$4563 \cdot s_{31} + 5723 \cdot s_{32}$	
	3/h.2s	s_{31}	3242	s_{32}	4733	$3242 \cdot s_{31} + 4733 \cdot s_{32}$	0.775
All							**0.738***

* Weighted by respective proportions of fish smolting at age 1, 2, and 3 (ocean contingent phenotype: 0.13, 0.81, 0.06; half-pounder phenotype: 0.34, 0.59, 0.07).



Appendix E. Results of sensitivity analysis for calculations in Appendix D: (a) 1/h.2s vs. 1/1.2s, (b) 2/h.2s vs. 2/1.2s, (c) 3/h.2s vs. 3/1.2s. Isopleths represent the relative lifetime fitness of the half-pounder life history ($W_{hp} \cdot W_{oc}^{-1}$) as a function of survivorship to the first spawning event (Pr [1st spawn]; range: 1.0^{-10} – 1.0) and survivorship from the first to the second spawning event (Pr [2nd spawn | 1st spawn]; range: 0.0 - 1.0)].