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## Potential Fitness Benefits of the Half-Pounder Life History in Klamath River Steelhead

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### Abstract

Steelhead *Oncorhynchus mykiss* from several of the world's rivers display the half-pounder life history, a variant characterized by an amphidromous (and, less often, anadromous) return to freshwater in the year of initial ocean entry. We evaluated factors related to expression of the half-pounder life history in wild steelhead from the lower Klamath River basin, California. We also evaluated fitness consequences of the half-pounder phenotype using a simple life history model that was parameterized with our empirical data and outputs from a regional survival equation. The incidence of the half-pounder life history differed among subbasins of origin and smolt ages. Precocious maturation occurred in approximately 8% of half-pounders and was best predicted by individual length in freshwater preceding ocean entry. Adult steelhead of the half-pounder phenotype were smaller and less fecund at age than adult steelhead of the alternative (ocean contingent) phenotype. However, our data suggest that fish of the half-pounder phenotype are more likely to spawn repeatedly than are fish of the ocean contingent phenotype. Models predicted that if lifetime survivorship were equal between phenotypes, the fitness of the half-pounder phenotype would be 17–28% lower than that of the ocean contingent phenotype. To meet the condition of equal fitness between phenotypes would require that first-year ocean survival be 21–40% higher among half-pounders in freshwater than among their cohorts at sea. We concluded that continued expression of the half-pounder phenotype is favored by precocious maturation and increased survival relative to that of the ocean contingent phenotype.

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Of the Pacific salmonids, steelhead *Oncorhynchus mykiss* arguably exhibit the most diverse array of life history patterns (Shapovalov and Taft 1954; Barnhart 1986; Busby et al. 1996). An unusual variant in this array is the “half-pounder” (Snyder 1925) life history. Half-pounders are steelhead that return to freshwater after only 2–4 months at sea, overwinter in freshwater, and return to the ocean the following spring (Snyder 1925; Kesner and Barnhart 1972). Half-pounders actively feed and rarely spawn while overwintering in freshwater (Kesner and Barnhart 1972; Everest 1973). For years this amphidromous (Myers 1949) migration was considered unique to steelhead from several river basins in northern California and south-

ern Oregon (Snyder 1925; Kesner and Barnhart 1972; Everest 1973); most notably the Klamath and Rogue basins, where incidence of the half-pounder life history averages 94% and 97% in fall-run stocks, respectively (Everest 1973; Hopelain 1998). However, similar expressions of life history have been observed in stocks endemic to Russia (Savvaitova et al. 2005) and in stocks introduced to Argentina (Pascual et al. 2001, 2002).

Although half-pounders have been studied since the early 20th century (e.g., Snyder 1925), the selective basis for the life history has not been established (Busby et al. 1994). Research has offered more lines of evidence against than for persistence of a half-pounder life history. For example, McPherson

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and Cramer (1982) and Hopelain (1998) reported a strong inverse relationship between incidence of the half-pounder life history and average length at first breeding. Because of the expected positive relationship between body size and breeding success in salmonids (van den Berghe and Gross 1989; Fleming et al. 1996; Blanchfield et al. 2003), the half-pounder migration should exact a significant breeding cost. Offsetting of costs through compensatory growth or increased postspawning survival has not been demonstrated. Kesner and Barnhart (1972), Everest (1973), and Savvaitova et al. (2005) found that only a small proportion (3.6–9.6%) of half-pounders spawned in the year of initial ocean entry. Unfortunately, each of these authors classified half-pounders in a different manner. Kesner and Barnhart (1972) defined half-pounders in the Klamath River as steelhead in the length-class of 250–349 mm; Everest (1973) defined half-pounders in the Rogue River as steelhead  $\leq 406$  mm in length; and Savvaitova et al. (2005) defined half-pounders in rivers of western Kamchatka (Russia) as steelhead that return to freshwater after spending only several months in brackish, coastal waters. In projecting a narrow size-criterion onto life history categories, Kesner and Barnhart (1972) omitted a subset of equal-age steelhead that would have reached lengths of almost 500 mm (Quinn and Myers 2004), and in doing so, probably underestimated incidence of maturation among Klamath River half-pounders. The need exists for a standardized classification of the half-pounder. Like Savvaitova et al. (2005), we suggest a life history-based, length-independent definition of half-pounders as steelhead that return to freshwater in the year of initial ocean entry. The criterion of ocean entry distinguishes the half-pounder from the estuary-ecotype of steelhead, which remains in an estuarine environment before overwintering in freshwater and later migrating to the ocean (Hayes et al. 2011).

Several hypotheses have been posited to account for existence of a half-pounder life history. Snyder (1925) suggested that all half-pounders re-enter freshwater on a maiden spawning migration; as noted above, this hypothesis has been rejected. Satterthwaite (1988) hypothesized that the half-pounder life history developed as a strategy to reduce ocean mortality. He observed that half-pounders strayed between basins at an 87% higher rate than adult steelhead and consequently concluded that there was greater adaptive value in emigrating from the ocean than in immigrating to natal streams. Satterthwaite (1988) also noted that among fish returning to a hatchery on the Rogue River, juvenile-to-adult survival was greater among stream-maturing steelhead (2.8%), almost all of which displayed the half-pounder life history, than among ocean-maturing steelhead (<1%), only 21% of which displayed the half-pounder life history (McPherson and Cramer 1982; Evenson and Ewing 1984, cited in Satterthwaite 1988). Because stream-maturing and ocean-maturing ecotypes differ in time at sea (stream-maturing steelhead return to freshwater several months earlier than ocean-maturing steelhead; Burgner et al. 1992; Busby et al. 1996), it is difficult to identify the period and rearing environment in which differential survival may have occurred. Savvaitova et al. (2005) suggested

that half-pounders represent a group of salinity-intolerant steelhead that are physiologically obligated to remain in brackish water; the authors did not offer an explanation for the return of half-pounders from the estuary to freshwater. Hodge (2010) concluded from otolith strontium isotope analysis that Klamath River half-pounders are tolerant of seawater; at least 52 of 54 half-pounders sampled had entered the ocean.

In accordance with evolutionary theory (e.g., Gross 1996; Gross and Repka 1998; Hendry et al. 2004), the persistence of a half-pounder life history requires that, at least on occasion, the half-pounder phenotype confer an advantage with respect to fitness, which is defined as “the lifetime summation of an individual’s probability of surviving to reproduce at any age multiplied by its fecundity (or male fertility) and breeding success at that age” (Gross 1987). If the incursion into freshwater increases survivorship, as suggested by Satterthwaite (1988), then the half-pounder migration may afford a selective advantage. Interestingly, Hopelain (1998) observed in the early 1980s that incidence of the half-pounder life history varied significantly among steelhead stocks of the lower Klamath River basin. Among fall-run steelhead, incidence ranged from 35.3% in the South Fork Trinity River to 100.0% in Horse and Clear creeks (tributaries of the middle Klamath). Even if ocean mortality is a driver of the half-pounder life history, expression of the phenotype may also be influenced by other fitness-related factors. Moreover, if steelhead from throughout the lower Klamath River basin experience similar ocean conditions, then among-stock differences in incidence must reflect inland conditions.

In this study we evaluated the relationship between expression of the half-pounder life history and subbasin of origin, sex, smolt length, smolt age, and spawning frequency in wild steelhead from the lower Klamath River basin (California). We also reexamined incidence of maturity among half-pounders, compared length and fecundity at age between fish of the half-pounder and alternate (ocean contingent) phenotypes, and compared incidence of the half-pounder life history between 1981 and 1983 (Hopelain 1998) and 2007–2009 (this study) to assess stability of the life history over time. Empirical data and outputs from a regional survival equation were used to parameterize simple life history models for female steelhead to explore fitness consequences of the half-pounder phenotype.

## METHODS

*Study site.*—The Klamath River drains 40,632 km<sup>2</sup> of southern Oregon and northern California before emptying into the Pacific Ocean (Figure 1). Historically, the Klamath River basin produced an estimated 650,000 to 1 million salmon per year (Gresh et al. 2000). However, salmon and steelhead production have declined significantly from historical levels and only a fraction of habitat within the basin is still accessible to anadromous fishes. Fish migration in the main stem is blocked 306 river kilometers (rkm) upstream of the Pacific Ocean by Iron Gate Dam. Below the dam, the Klamath is fed by numerous small tributaries

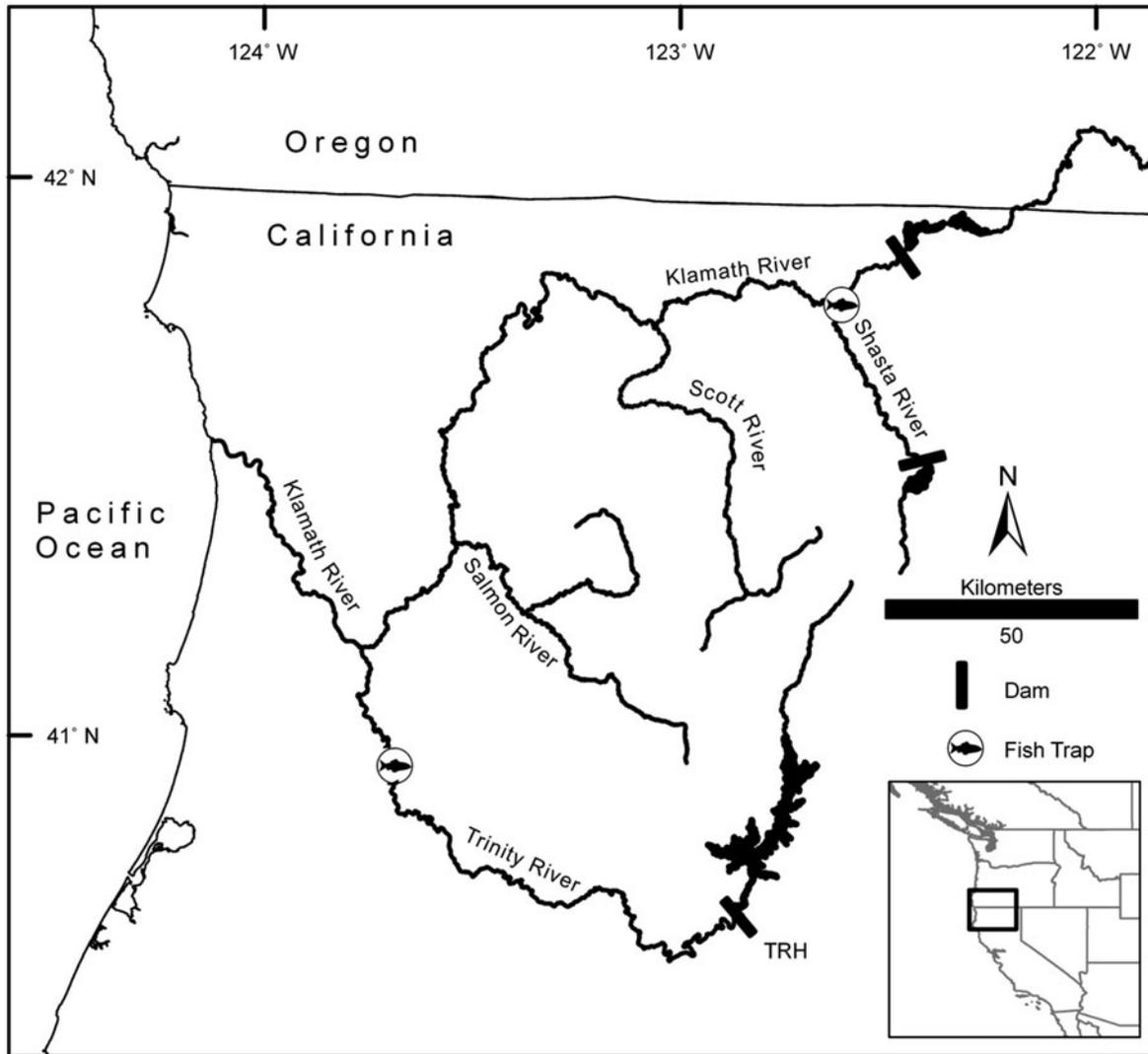


FIGURE 1. Map of the steelhead study area showing the locations of fish traps, barriers to anadromy, and Trinity River Hatchery (TRH).

and four major tributaries: the Trinity, Salmon, Scott, and Shasta rivers. Anadromous migrations in the Trinity and Shasta rivers are blocked by Lewiston and Dwinnel dams 180 and 65 river kilometers (rkm), respectively, upstream of their confluences with the Klamath. In addition to supporting steelhead, the lower Klamath River basin supports populations of other anadromous fishes, including spring- and fall-run Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, Coastal Cutthroat Trout *O. clarkii clarkii*, Green Sturgeon *Acipenser medirostris*, Pacific Lamprey *Entosphenus tridentatus*, Eulachon *Thaleichthys pacificus*, and Threespine Stickleback *Gasterosteus aculeatus*.

**Fish capture.**—Fish capture and handling was performed under the auspices of Humboldt State University IACUC Protocol 06/07 F 175A. From August 2007 through April 2009, wild steelhead were captured throughout the lower Klamath River basin with hook and line and at weir trapping facilities operated by the California Department of Fish and Wildlife

(CDFW). Hook-and-line sampling was conducted from August through April of each year. Steelhead were trapped and systematically subsampled at the Willow Creek weir on the Trinity River (rkm 35) in August–November of 2007 and 2008. Steelhead were trapped and sampled at the Shasta River weir (rkm 1) in October–December 2008. Weirs were effective at capturing steelhead >350 mm FL (W. Sinnen, CDFW, personal communication).

**Scale collection and analysis.**—After fish were confirmed to be of wild origin by the absence of clipped fins and clipped maxillaries, their fork lengths (mm; but cm for those at weirs), sex, date, and location of capture were recorded. Scales were removed for analysis 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.

Life histories of steelhead were determined through visual examination of scales in accordance with the methods of Davis

TABLE 1. Examples of the notation system (Hopelain 1998) used to report steelhead life history. A forward 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.

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

and Light (1985). After life history landmarks were identified in scale patterns, image analysis software (Image Pro Plus; Media Cybernetics, Bethesda, Maryland) was used to measure distances ( $\mu\text{m}$ ) between landmarks and the scale focus. Lengths at life history landmarks and growth increments between landmarks were back-calculated to the nearest millimeter using the Fraser–Lee method (Fraser 1916; Lee 1920; Carlander 1982).

Steelhead were classified as half-pounders if their sea age at capture was  $\leq 1$  year and as adults if it was  $\geq 1$  year. For fish captured in fall or early winter, reported age included the subsequent winter annulus. Life history was reported according to the methods of Hopelain (1998), who adapted Shapovalov and Taft's (1954) system of notation for inclusion of the half-pounder phenotype. Life history categories were distinguished by number of years in freshwater, presence–absence of a half-pounder stage, number of years at sea, and number of spawning events (Table 1). Incidence rates of the half-pounder phenotype were derived from analysis of adult steelhead scales. We compared incidence rates between our study and Hopelain (1998) via the binomial proportions test (BPT). All calculations and statistical analyses hereafter were performed in R (R Core Team 2010) at  $\alpha = 0.05$ .

*Maturation in half-pounders.*—To determine the sex and incidence of maturity in half-pounders, gonads were extracted from a time- and size-stratified subsample of half-pounders captured with hook and line. Gonads were weighed to the nearest hundredth of a gram and examined under a dissecting microscope ( $3\times$ ). Immature females were identified by gonads with an anterior thickening, triangular cross-section, and granular appearance, while immature males were identified by gonads with a smooth, thread-like appearance. Mature females were identified by ovaries with visibly developed eggs and combined weight exceeding 1.00 g, while mature males were identified by testes with a whitish, lobular appearance and combined weight exceeding 1.00 g (Kesner and Barnhart 1972).

Because the subsample of half-pounders did not necessarily reflect the age and size distribution of the population, we developed a predictive model to estimate the incidence of maturation.

Our interest was in factors influencing the onset of maturation, so we focused on predictor variables that preceded capture and assessment of maturity. Based on initial examination of data, six biological parameters were included in analysis of factors related to incidence of maturity in half-pounders: sex, smolt age, two length-at-age metrics (at the last freshwater winter, at ocean entry), and two growth ( $\Delta$  length) metrics (between the last freshwater winter and freshwater reentry, between ocean entry and freshwater reentry). To evaluate relationships between predictor variables and incidence of maturation, we used the six biological parameters to construct six single-predictor logistic regression models. Models were ranked using Akaike's information criterion (AIC; Akaike 1974; Burnham and Anderson 2002). The lower ranking length-at-age and growth metrics were eliminated from further consideration to avoid inclusion of highly correlated parameters. The three best-supported predictor variables—length at the last freshwater winter, smolt age, and growth between the last freshwater winter and freshwater reentry—were used to construct a second series of logistic regression models. Because there was no a priori evidence of interaction between predictor variables, we did not include interaction terms. Candidate models were ranked using AIC. The best-fitting model was used to generate maturation probabilities.

*Half-pounder life history.*—To isolate trade-offs in the half-pounder life history, we compared length and fecundity at age between steelhead that exhibited parallel life history trajectories (i.e., pathways that differed only in the presence of a half-pounder stage; Table 1). Groups were compared statistically with ANOVA and binomial proportions tests. To evaluate potential fecundity-related fitness costs of alternate life history trajectories, egg number was estimated with an empirically derived regression model. Length and fecundity data were collected from female steelhead to quantify the relationship between body size and reproductive output. In the interest of minimizing the impact on the wild population, we collected the majority of samples from steelhead returning to the Trinity River Hatchery in January and February 2008. Length and fecundity data were also collected from a small subset of wild steelhead captured via

TABLE 2. Life history table for alternative phenotypes, where  $s_x$  is the probability of surviving from age  $x$  (ocean winter  $x - 1$ ) to age  $x + 1$  (ocean winter  $x$ ),  $l_x$  is the fraction of individuals that survive from birth to at least age  $x$ ,  $b_x$  is breeding success at age  $x$  (as approximated by fecundity),  $p$  is the proportion of half-pounders that spawn in the year of initial ocean entry, and fitness is the sum of products ( $\sum l_x b_x$ ); OE = ocean entry and OW = ocean winter.

Half-pounder					Ocean contingent				
Age ( $x$ )	$s_x$	$l_x$	$b_x$	$l_x \cdot b_x$	Age ( $x$ )	$s_x$	$l_x$	$b_x$	$l_x \cdot b_x$
OE	$s_1$	$s_0$	0	0	OE	$s_1'$	$s_0$	0	0
OW1	$s_2$	$s_0 s_1$	$b_1$	$p(s_0 s_1 b_1)$	OW1	$s_2$	$s_0 s_1'$	0	0
OW2	$s_3$	$s_0 s_1 s_2$	$b_2$	$s_0 s_1 s_2 b_2$	OW2	$s_3$	$s_0 s_1' s_2$	$b_2'$	$s_0 s_1' s_2 b_2'$
OW3	$s_4$	$s_0 s_1 s_2 s_3$	$b_3$	$s_0 s_1 s_2 s_3 b_3$	OW3	$s_4$	$s_0 s_1' s_2 s_3$	$b_3'$	$s_0 s_1' s_2 s_3 b_3'$
$\sum l_x b_x$		$p s_0 s_1 b_1 + s_0 s_1 s_2 b_2 + s_0 s_1 s_2 s_3 b_3$			$\sum l_x b_x$		$s_0 s_1' s_2 b_2' + s_0 s_1' s_2 s_3 b_3'$		

hook and line. Data from both hatchery and wild steelhead were  $\log_e$  transformed, and fecundity was regressed on length. We used ANCOVA to evaluate the fit of wild fish to the hatchery-derived model.

To model fitness consequences of the half-pounder life history, we applied Gross's (1987) definition of fitness, a computational equivalent to the per-generation ratio of increase (Brommer 2000; McMahon et al. 2003) (Table 2). Because fitness consequences of alternative tactics are best evaluated by considering one tactic relative to another (Hendry et al. 2004), we compared three sets of parallel life history trajectories through three ocean winters (sample sizes were insufficient for comparison through four or more ocean winters). Because the fitness value of a tactic is typically estimated as the average value for individuals expressing the tactic (Sober 2001), we used average female fecundity, as derived from the length–fecundity regression model, as a proxy for breeding success in each phenotype. First, we estimated the relative fitness of the half-pounder phenotype ( $W_{hp}/W_{oc}$ ) under the condition that lifetime survivorship was equal between alternate phenotypes, i.e.,

$$\frac{W_{hp}}{W_{oc}} = \frac{p b_1 + s_2 b_2 + s_2 s_3 b_3}{s_2 b_2' + s_2 s_3 b_3'} \quad (1)$$

where  $p$  is the proportion of half-pounders that spawn in the year of initial ocean entry,  $s_x$  is the probability of surviving from ocean winter  $x - 1$  to ocean winter  $x$ , and  $b_x$  and  $b_x'$  are the breeding success of the half-pounder and ocean contingent phenotypes at ocean winter  $x$ , respectively. Next, we estimated the relative first-year ocean survival of the half-pounder phenotype ( $s_1/s_1'$ ) under the condition of equal fitness between alternate phenotypes and under the condition that the survival of alternate phenotypes differed only during the first ocean winter (when half-pounders were in freshwater and ocean contingents were at sea), i.e.,

$$\frac{s_1}{s_1'} = \frac{s_2 b_2' + s_2 s_3 b_3'}{p b_1 + s_2 b_2 + s_2 s_3 b_3} \quad (2)$$

We derived baseline estimates of  $s_2$  (survival between the first and second ocean winters) by entering observed length-at-age data into a regional model of length-dependent ocean (smolt-to-adult) survival (Satterthwaite et al. 2009; Table 3). Because marine mortality of Pacific salmonids is typically greatest during the first year at sea (Beamish and Mahnken 2001; Beamish et al. 2004; Melnychuk et al. 2007), smolt-to-adult survival should, in theory, be a conservative estimate for survival of steelhead between the first and second ocean winters. We derived baseline estimates of  $s_3$  (secondary or postspawning survival) by dividing the number of age  $x$  smolts spawning at ocean winter three by the number of age  $x$  smolts spawning at ocean winter two. We assumed for simplicity that precocious spawning by half-pounders had no effect on subsequent survival and fecundity. However, because mature half-pounders presumably expend more energy during their first ocean winter than immature half-pounders expend during their first ocean winter, this may have resulted in an overestimation of subsequent survival by precocious spawners. To calculate age-structured estimates of relative fitness and

TABLE 3. Baseline and alternative survival parameters used in fitness models ( $s_x$  is the probability of surviving from ocean winter  $x - 1$  to ocean winter  $x$ ). Estimates of  $s_2$  were derived by feeding our observed length-of-ocean-entry data (smolt age 1 = 190 mm, smolt age 2 = 211 mm, and smolt age 3 = 219 mm) into a model from Satterthwaite et al. (2009), i.e.,  $s = 0.84[(e^{-8.657 + 0.0369l})/(1 + e^{-8.657 + 0.0369l})]$ , where  $s$  is the estimated smolt-to-adult survival and  $l$  is length at ocean entry. The sources for  $s_3$  were our estimates of secondary (postspawning) survival as derived by dividing the number of age- $x$  smolts spawning in ocean winter three by the number of age- $x$  smolts spawning in ocean winter two.

Parameter	Baseline value	Variants (%)
$s_2$		
Smolt age 1	0.136	-50, +100
Smolt age 2	0.248	-50, +100
Smolt age 3	0.302	-50, +100
$s_3$		
Smolt age 1	0.189	-50, +100
Smolt age 2	0.128	-50, +100
Smolt age 3	0.053	-50, +100

survival, we weighted the results according to the proportions of steelhead smolting at ages 1, 2, and 3 (half-pounder phenotype: 0.34, 0.59, and 0.07; ocean contingent phenotype: 0.13, 0.81, and 0.06). To evaluate the sensitivity of results to estimated parameters, we recalculated relative fitness and relative first-year ocean survival while allowing nominal probabilities of second-year and third-year ocean survival to increase and decrease by as much as 100% and 50%, respectively (i.e., we doubled and halved the baseline estimates).

**RESULTS**

**Fish Capture**

Half-pounders were captured continuously from August through April, with peak numbers occurring in the main-stem Klamath River in August–October. Half-pounders were captured in the main stem and in all four of the major tributaries. The location of capture ranged from <16 rkm to >285 rkm upstream of the river’s outlet into the Pacific Ocean. Among half-pounders, fork length at capture ranged from 256 to 525 mm (mean = 358 mm, SE = 4) and weight from 172 to 986 g (mean = 426 g, SE = 17). Of the 245 fish for which sex could be determined, 116 were male and 129 were female.

**Maturation in Half-Pounders**

Although the majority of half-pounders were immature, we observed precocious sexual maturation in both males and females. Sex and state of maturity were classified for 100 half-pounders (46 males, 54 females); of these, 12 were sexually mature (4 males, 8 females; mean FL = 383 mm). Gonad weight was greater in mature specimens than in immature specimens (18.49 ± 7.239 [mean ± SE] versus 0.31 ± 0.02 g; ANOVA:  $F_{1,97} = 49.06, P < 0.001$ ). Incidence of maturation did not differ significantly between sexes ( $\chi^2 = 0.40, df = 1, n = 100, P = 0.529$ ). Of the models considered for predicting incidence of maturation in half-pounders, the best-fitting model included only one parameter: length at the last freshwater winter (Table 4). Length at the last freshwater winter was greater among mature half-pounders than among immature half-pounders (216 ± 10 mm versus 141 ± 4 mm; ANOVA:  $F_{1,96} = 52.96, P < 0.001$ ). We used the best-fitting model to estimate the probability of maturation in half-pounders, that is,

$$P = \frac{e^{(\alpha+\beta \cdot l)}}{1 + e^{(\alpha+\beta \cdot l)}}, \tag{3}$$

where  $P$  is the probability of maturing in the year of initial ocean entry,  $\alpha = -15.0241$  (SE = 3.6130),  $\beta = 0.0727$  (SE = 0.0185), and  $l$  is length at the last freshwater winter (Figure 2). The jackknife (leave-one-out cross-validation) classification accuracy of this model was 93%. Retrospective application of this model to a random sample of adult steelhead ( $n = 92$ ) suggests

TABLE 4. Summary of candidate binary response models for predicting the incidence of maturity in half-pounders from the lower Klamath River basin. Models were ranked according to Akaike’s information criterion (AIC;  $\Delta$ AIC = AIC differences,  $w_i$  = Akaike weights). Predictor variables included fork length at the last freshwater winter (FLFW), growth (the change in length) between the last freshwater winter and freshwater reentry (GROW), and smolt age (AGE).

Model	AIC	$\Delta$ AIC	$w_i$
FLFW	37.196	0.000	0.365
FLFW + GROW	37.318	0.122	0.343
FLFW + GROW + AGE	38.895	1.699	0.156
FLFW + AGE	39.177	1.981	0.136
AGE	62.396	25.199	0.000
GROW + AGE	64.364	27.168	0.000
GROW	76.167	38.971	0.000

that approximately 8% of half-pounders spawn during their first ocean winter.

**Factors Associated with Half-Pounder Life History**

The incidence of the half-pounder life history differed among subbasins and over time (Table 5). The half-pounder phenotype was more prevalent in the basin above the Trinity confluence than in the Trinity subbasin alone (91.6% versus 11.0%;  $\chi^2 = 200.21, df = 1, n = 375, P < 0.001$ ). In the Trinity River subbasin, incidence of the half-pounder life history was lower among fall-run steelhead in 2007–2008 than in 1982 ( $\chi^2 =$

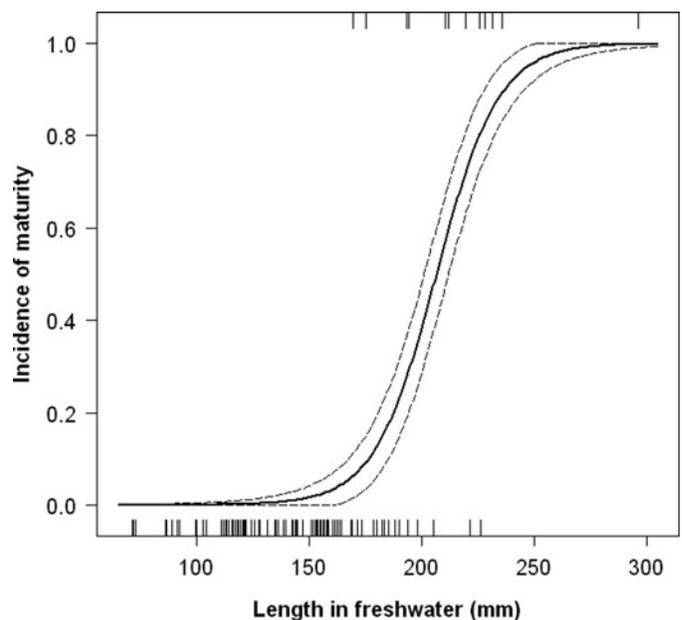


FIGURE 2. Observed and predicted incidence of maturity in half-pounders versus fork length in the winter preceding ocean entry. The tick marks at the top denote mature fish, those at the bottom immature fish. The solid line depicts the estimated probability of maturation; the dashed lines denote the 95% confidence interval around that line.

TABLE 5. Incidence of the half-pounder life history among adult steelhead sampled in the lower Klamath River basin in 2007–2009 (this study) and in the early 1980s (Hopelain 1998).

River	Years	Sample size	Incidence of half-pounder trait (%)				All
			Spawning trip				
			1st	2nd	3rd	4th	
Klamath	2007–2009	63	96.3	100.0	100.0		96.8
Trinity	2007–2008	291	6.9	36.8	14.3		11.0
	1982	45	96.8	42.9			80.0
Salmon	2008–2009	11	71.4	0.0	50.0	100.0	58.3
	1981–1983	15	90.9	75.0			86.7
Scott	2008	4	75.0				75.0
	1981–1983	78	96.5	94.1	100.0	100.0	96.1
Shasta	2008	8	100.0	100.0			100.0
	1981–1983	119	95.2	88.6	100.0		94.1
All	2007–2009	377	26.4	46.8	36.4	100.0	29.2

110.72,  $df = 1$ ,  $n = 336$ ,  $P < 0.001$ ). Because sample sizes from the other three major tributaries were limited, data were pooled to compare current and historical figures from above the Trinity confluence; there, incidence of the half-pounder life history did not change between 1981–1983 and 2007–2009 (94.3% versus 90.4%;  $\chi^2 = 1.13$ ,  $df = 1$ ,  $n = 467$ ,  $P = 0.287$ ).

Overall, neither smolt length ( $204 \pm 5$  mm [mean  $\pm$  SE] versus  $206 \pm 2$  mm; ANOVA:  $F_{1,360} = 0.228$ ,  $P = 0.633$ ) nor sex ratio (51.5% male versus 44.2% male;  $\chi^2 = 1.25$ ,  $df = 1$ ,  $n = 341$ ,  $P = 0.263$ ) were related to the presence–absence of the half-pounder life history. Smolt age was lower among fish displaying the half-pounder phenotype than among fish displaying the ocean contingent phenotype ( $1.73 \pm 0.06$  years versus  $1.93 \pm 0.03$  years; ANOVA:  $F_{1,337} = 11.93$ ,  $P < 0.001$ ). Within the Trinity River subbasin, smolt length was smaller ( $181 \pm 6$  mm versus  $206 \pm 2$  mm; ANOVA:  $F_{1,282} = 16.57$ ,  $P < 0.001$ ) and smolt age was lower ( $1.52 \pm 0.11$  years versus  $1.93 \pm 0.03$  years; ANOVA:  $F_{1,266} = 20.79$ ,  $P < 0.001$ ) for fish that exhibited the half-pounder life history than for fish that remained at sea in the year of initial ocean entry. For the rest of the basin, small and unbalanced sample sizes precluded rigorous comparisons between groups, though summary statistics illustrate general trends. In the basin above the Trinity confluence, smolt length was generally greater among fish of the half-pounder phenotype than among fish of the ocean contingent phenotype ( $214 \pm 6$  mm versus  $208 \pm 18$  mm), whereas the converse was true for smolt age ( $1.82 \pm 0.07$  years versus  $2.00 \pm 0.26$  years).

### Length–Fecundity Relationships

Reproductive output was positively and significantly related to fork length in both wild and hatchery steelhead. Among 108 hatchery fish (FL:  $624 \pm 3$  mm; fecundity:  $5,008 \pm 115$  eggs), total ovarian output (volume) was positively correlated with

fork length ( $F_{1,106} = 224.60$ ,  $P < 0.001$ ,  $r^2 = 0.68$ ). Fecundity was positively correlated with fork length ( $F_{1,106} = 65.49$ ,  $P < 0.001$ ,  $r^2 = 0.38$ ), as described by

$$\text{fecundity} = \alpha \cdot \text{FL}^\beta, \quad (4)$$

where  $\alpha = 0.2128$  (95% confidence limits, 0.0615 and 0.7359) and  $\beta = 2.4301$  (SE = 0.3003). The fecundity of 10 wild fish (FL:  $494 \pm 29$  mm; fecundity:  $3,249 \pm 602$  eggs) was well predicted by this hatchery-derived model. Data collected from wild fish fell within a 95% prediction interval on the fitted hatchery model and slopes of the individual regression lines for fecundity versus fork length did not differ between wild and hatchery fish ( $t = -0.14$ ,  $P = 0.888$ ).

### Consequences of the Half-Pounder Life History

Comparison between fish of the half-pounder and ocean contingent phenotypes revealed differences in length and fecundity at age as well as potential differences in patterns of iteroparity. In the first year at sea (i.e., between the time of initial ocean entry and the end of the first ocean winter), steelhead that remained in the ocean grew an average of 288 mm (SE = 3 mm, range = 92–400 mm), whereas half-pounders grew an average of 145 mm (SE = 3 mm, range = 73–261 mm). Consequently, fish of the ocean contingent phenotype were significantly larger than fish of the half-pounder phenotype at the end of the first and second ocean winters and were still marginally larger at the end of the third ocean winter (Table 6). After the first ocean winter, individuals displaying the half-pounder phenotype grew faster than fish displaying the ocean contingent phenotype, indicating some level of compensatory growth. Nevertheless, the extra growth accrued in the first year at sea afforded ocean contingents a fecundity advantage at the second and third ocean winters (typically the first and second spawning events; Figure 3). Incidence

TABLE 6. Comparison of fork length at age (mean ± SE) between parallel life history trajectories (i.e., pathways that differ only in the presence of a half-pounder migration) and results of one-way ANOVA (OE = ocean entry, OW = ocean winter, *n* = 309).

Life history stage	FL (mm) <sup>a</sup>		<i>P</i>
	<b>1/h.2s</b>	<b>1/1.2s</b>	
OE	173 ± 7	203 ± 6	0.002
OW1	341 ± 6	466 ± 9	<0.001
OW2	512 ± 13	592 ± 6	<0.001
OW3	587 ± 26	648 ± 16	0.086
	<b>2/h.2s</b>	<b>2/1.2s</b>	
OE	226 ± 7	207 ± 2	0.011
OW1	369 ± 6	501 ± 3	<0.001
OW2	509 ± 6	602 ± 3	<0.001
OW3	574 ± 9	640 ± 9	<0.001
	<b>3/h.2s</b>	<b>3/1.2s</b>	
OE	229 ± 16	214 ± 8	0.414
OW1	398 ± 22	496 ± 17	0.004
OW2	526 ± 10	603 ± 13	<0.001
OW3	615	NA	NA

<sup>a</sup>A lowercase h denotes a half-pounder run and a lowercase s denotes a spawning run. A forward slash (/) separates years in freshwater (left) from years in saltwater (right) and a period (.) separates growing years from spawning years.

of the half-pounder life history varied with reproductive history. Incidence was significantly higher in second-time spawners than in first-time spawners (46.8% versus 26.4%;  $\chi^2 = 7.30$ , *df* = 1, *n* = 365, *P* = 0.007), and while small sample size precluded rigorous analysis, incidence was also higher in third-time spawners (36.4%, *n* = 11) than in first-time spawners (Table 5).

The first fitness exercise suggested that if overall survivorship was equal between alternate phenotypes, the lifetime fitness of the half-pounder phenotype would be approximately 72% of that of the ocean contingent phenotype. Sensitivity analysis revealed that as long as survivorship was equal between alternate phenotypes, the absolute value of survival parameters had little influence on relative fitness estimates. For example, reducing survival parameters by 50% increased relative fitness of the half-pounder phenotype by only 9%. The second exercise suggested that to meet the condition of equal fitness between alternate phenotypes, first-year ocean survival of half-pounders must be approximately 140% that of ocean contingents. This result was not sensitive to late-stage survival parameters; doubling both second-year and third-year ocean survival increased relative first-year ocean survival of half-pounders by only 7%.

Given evidence that the incidence of the half-pounder life history was higher among repeat spawners than among maiden spawners, we conducted additional a posteriori iterations of both fitness exercises to explore whether the half-pounder phenotype provides latent benefits in survivorship (i.e., results in additional breeding opportunities). We estimated relative fitness of the half-pounder phenotype under the conditions that survivorship through the second ocean winter is equal between paral-

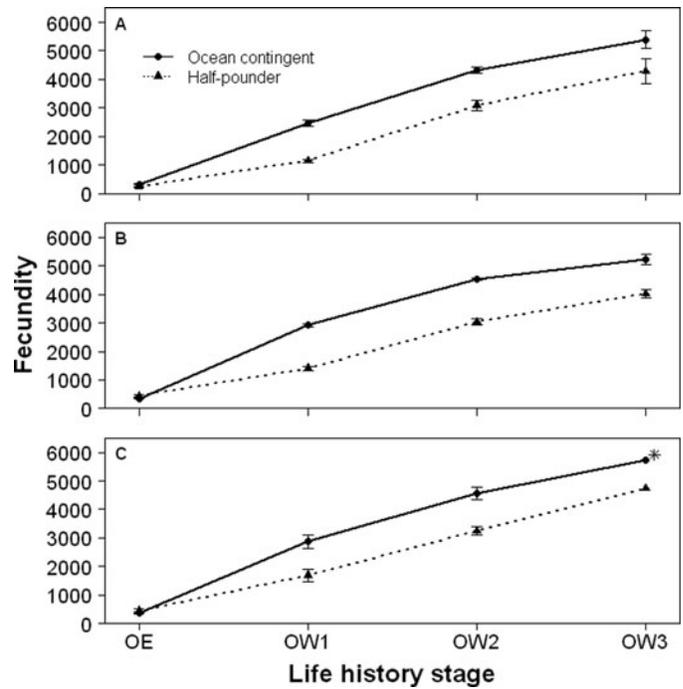


FIGURE 3. Comparison of estimated mean fecundity (error bars = SEs) between fish of the half-pounder and ocean contingent phenotypes for fish of (A) smolt age 1 (1/h.2s versus 1/1.2s; see Tables 1 or 6 for abbreviations), (B) smolt age 2 (2/h.2s versus 2/1.2s), and (C) smolt age 3 (3/h.2s versus 3/1.2s). Fecundity was estimated according to the equation  $\text{fecundity} = \alpha \cdot \text{FL}^\beta$ , where  $\alpha = 0.2128$  (95% confidence limits, 0.0615 and 0.7359) and  $\beta = 2.4301 \pm 0.3003$  (mean ± SE). The asterisk denotes a projected point (i.e., one for which we had no observed length-at-age data); OE = ocean entry, OW = ocean winter; *n* = 309).

lel life histories and that secondary or postspawning survival (survivorship from the second to third ocean winters) differs between alternate phenotypes. We also estimated relative first-year ocean survival under the conditions that fitness is equal between phenotypes and that survivorship differs, both during the first ocean winter and from the second to third ocean winters. Postspawning survival was calculated by dividing the number of first-time spawners of a particular phenotype by the number of second-time spawners of that same phenotype (half-pounder: 22 of 84 = 0.262; ocean contingent: 25 of 234 = 0.107).

Inclusion of differential postspawning survival into model runs changed the magnitude but not the direction of our results. The third exercise suggested that if estimates of secondary survival were realized, lifetime fitness of the half-pounder phenotype would be approximately 83% that of the ocean contingent phenotype. Sensitivity analysis suggested that variations in secondary survival had relatively little influence on results. Reducing postspawning survival of both phenotypes by 50% reduced the estimate of relative fitness by only 6%. To reach the point of equal fitness between alternate phenotypes required that secondary survival for the half-pounder phenotype be at least threefold that of the ocean contingent phenotype. The fourth exercise suggested that if estimates of secondary survival were

realized, first-year ocean survival of half-pounders must be 121% that of ocean contingents to meet the condition of equal fitness. This result was relatively insensitive to concordant changes to parameters; doubling secondary survival of both phenotypes reduced relative fitness by only 12%.

## DISCUSSION

Our findings are consistent with the findings of earlier studies with regard to the run timing and mean body size of half-pounders. We observed peak numbers of half-pounders in the Klamath River from August through October; Everest (1973) reported that most half-pounders re-entered the Rogue River in August and September. We calculated that mean length of half-pounders was 358 mm; Everest (1973) reported a mean length of 356 mm. Presumably, because we did not consider length at capture as a defining criterion, we observed a larger range in length at capture of half-pounders (256–525 mm) than was reported by others: 250–349 mm by Kesner and Barnhart (1972), 206–406 mm (as interpreted from a length-frequency histogram) by Everest (1973), and 250–410 mm (Hopelain 1998).

Our study extends observations of precocious maturation among salmonids in one important way, in that we observed similar rates of precocious maturation in male and female steelhead. Incidence of precocious development is typically higher among male salmonids (Willson 1997; Quinn and Myers 2004) because the breeding-related benefits of increased body size are greater for females than for males (Fleming et al. 1996; Thériault et al. 2007). Kesner and Barnhart (1972) observed equal numbers of sexually mature males (jacks) and females (jills) (6 of each) among steelhead returning to the Klamath River in the year of initial ocean entry (i.e., half-pounders,  $n = 202$ ). However, 0 of 3 and 1 of 19 sexually mature half-pounders observed by Everest (1973) and Savvaitova et al. (2005), respectively, were female. Reproductive investment by female salmonids is typically inversely related to postspawning survival (Crespi and Teo 2002). Thus, one might expect that precocious maturation of female steelhead is indicative of low levels of repeat spawning. Nevertheless, reproductive histories in the lower Klamath River basin were generally consistent with regional values. For example, we observed that among adult steelhead 84.3% were first-time spawners, 12.5% were second-time spawners, 2.9% were third-time spawners, and 0.3% were fourth-time spawners; Shapovalov and Taft (1954) reported corresponding values of 82.8, 15.0, 2.1, and <1.0% in steelhead from Waddell Creek, California.

Our finding that juvenile length was related to incidence of maturity in half-pounders is consistent with other studies reporting a positive relationship between length at age and precocious maturation (e.g., Vøllstad et al. 2004; Shearer et al. 2006). Others observed that among half-pounders, mature fish were generally the largest individuals of the group: >349 mm FL (Kesner and Barnhart 1972) and 380 mm FL (Everest 1973). Appleby et al. (2003) demonstrated that the frequency of jacks within a co-

hort of Coho Salmon could be increased by increasing smolt size. Incidence of sexual maturity among half-pounders may respond similarly to increasing smolt size and, thus, to increasing freshwater productivity. However, like the incidence of jacking in salmon, the incidence of precocious maturation in half-pounders may be under frequency-dependent selection (Gross 1985; Berejikian et al. 2010). That fork length at the last freshwater winter better predicted maturation in half-pounders than did fork length at ocean entry (among other variables) suggests that the developmental switch-point (Mangel 1994; Thorpe et al. 1998)—i.e., to mature or not to mature—may be reached while an individual is still in freshwater. This suggestion coincides with the finding by Vøllstad et al. (2004) that size prior to ocean entry had a significant influence on the tendency for jacking in both Coho and Chinook salmon. Thorpe (1994) suggested that Atlantic Salmon *Salmo salar* reach the maturation switch-point some 12 months prior to a potential breeding event.

Our results suggest that subbasin of origin and smolt age are related to incidence of the half-pounder life history; however, the degree to which the subbasin and smolt age relationships reflect genetic or environmental factors, or an interaction of the two, remains unknown. Results of an informal breeding experiment suggest that both genetic and environmental components influence expression of the half-pounder life history. By selecting against the half-pounder phenotype, managers at the Cole M. Rivers Hatchery on the Rogue River were able to create a broodstock in which incidence of the life history was relatively low [Evenson (Oregon Department of Fish and Wildlife, personal communication), cited by Busby et al. 1994]. However, subsequent increases in incidence of the half-pounder life history coincided with increases in hatchery growth rates (Cramer et al. 1985). Interestingly, Peterson (2011) observed the inverse relationship in steelhead from Trinity River Hatchery, where a decline in incidence of the half-pounder life history (from 75% in 1980 to <10% in 2006–2008) coincided with an increase in mean weight at release of hatchery smolts (from 55.3 g in 1979–1991 to 99.4 g in 1992–2007). Overall, our findings regarding the relationship between the half-pounder life history and length at age are consistent with the pattern observed in the Rogue River (Cramer et al. 1985). Steelhead in the Trinity River exhibited the smallest length at ocean entry and the lowest incidence of the half-pounder life history, whereas steelhead from the Shasta River exhibited the greatest length at ocean entry and the highest incidence of the half-pounder life history. The relationship between smolt length and incidence of the half-pounder life history differed between the Trinity River subbasin and all other subbasins, which suggests that the link between growth and expression of life history might be complex.

Several findings lead us to the conclusion that continued expression of a half-pounder life history is favored by precocious maturation and increased ocean survival relative to that of the ocean contingent phenotype. First, approximately 8% of half-pounders spawn while overwintering in freshwater. This precocious spawning presumably offers mature fish of the

half-pounder phenotype a significant advantage in the event of low second-year and third-year ocean survival. Second, that most half-pounders return to freshwater in an immature state, months after the potential maturation switch point, suggests that the fitness-related benefit of the life history is typically unrelated to precocious spawning. If the half-pounder migration afforded a benefit only to mature half-pounders, only mature half-pounders would return to freshwater in their first year at sea. Third, models predicted that alternate phenotypes will approach equal fitness only when breeding-related costs of the half-pounder migration are offset by survival-related benefits of the half-pounder migration. That the incidence of the half-pounder life history did not change significantly (from 1981–1983 to 2007–2009) in the basin above the Trinity confluence suggests that this condition has been met on one or more occasions. In contrast, the apparent decline in incidence in the Trinity River subbasin (also see Peterson 2011) suggests that breeding-related fitness costs frequently, or at least recently, outweighed survival-related fitness benefits. Last, models predicted that if lifetime survivorship was equal between alternate phenotypes, the half-pounder life history would afford no fitness benefit to individuals that express the phenotype. Persistence of a half-pounder life history (since at least 1925) is evidence to the contrary. Persistence requires that, on occasion, lifetime survivorship be higher and fitness be equal or greater among half-pounders than among fish of the ocean contingent phenotype.

While our results suggest that secondary survival is higher among fish of the half-pounder phenotype than among fish of the ocean contingent phenotype, the models predicted that the fitness-related benefits of increased postspawning survival are not enough to offset breeding-related costs of the half-pounder migration. Further, while the conceptual link between survival and fitness is clear, it is unclear how an amphidromous migration during the first ocean winter would manifest into a survival-related benefit between the second and third ocean winters. A more intuitive explanation for persistence of a half-pounder life history is that the incursion into freshwater during the first ocean winter increases the probability that an individual will survive to the second and subsequent ocean winters. Smith and Slaney (1980) observed a 56% rate of survival among subadult (i.e., immature) anadromous Dolly Varden *Salvelinus malma* overwintering in freshwater.

Because expression of the half-pounder life history is probably influenced by selective forces, the incidence of the half-pounder life history should vary with the relative costs and benefits of expression. For example, a cycle of strong ocean upwelling coincident with poor inland conditions might lead to a decline in expression of the half-pounder phenotype, whereas the converse situation might lead to an increase in expression of the phenotype. If all wild steelhead from the lower Klamath River basin experience similar ocean conditions, then the aberrantly low incidence of the half-pounder phenotype among Trinity stocks is probably a function of conditions in the Trin-

ity River subbasin. Further, the observed decline in incidence between 1982 and 2007 probably reflects changes in the basin.

The concurrent decline in the incidence of the half-pounder life history among both wild and hatchery stocks from the Trinity River subbasin suggests that selection against the half-pounder phenotype acts at the subbasin scale. Based on their evaluation of salmonid population trends in the lower Klamath River basin, Quiñones et al. (2013) suggested that wild salmon and steelhead may be replaced by their hatchery-produced counterparts. If hatchery practices result both in inadvertent selection against the half-pounder phenotype (Peterson 2011) and inadvertent replacement of wild steelhead by hatchery steelhead (Quiñones et al. 2013), the half-pounder life history could be unintentionally culled from a population. The Trinity River hosts the lower Klamath River basin's largest hatchery steelhead component (20–34%; Busby et al. 1994) and the basin's lowest incidence of the half-pounder life history. Given evidence that first-year ocean survival is size-dependent (Ward et al. 1989; Bond et al. 2008) and that the half-pounder migration increases first-year overwinter survival, it is curious that incidence of the half-pounder life history is lowest in the basin with the smallest length at ocean entry. Our findings suggest that anthropogenic selection against the half-pounder phenotype could have unintended, negative consequences.

That the half-pounder life history is displayed by only a few of the world's steelhead populations suggests that fish from these populations encounter a suite of environmental conditions that differ from conditions elsewhere. Still unidentified are commonalities among half-pounder-bearing streams of northern California–southern Oregon, eastern Russia, and southeastern Argentina. Everest (1973) suggested that steelhead from the Rogue and Klamath rivers share a common, productive rearing environment in the ocean. That the half-pounder life history is prevalent in Klamath and Rogue River stocks, but absent from neighboring steelhead populations (e.g., Smith and Chetco rivers, which presumably utilize the same offshore areas), suggests that natal origin has an equal or greater influence on expression of the half-pounder history than does ocean rearing.

Comparison between the Klamath River and other half-pounder-bearing streams reveals a number of differences and fewer similarities. For example, the Klamath River is 463 km long and originates in high desert; the half-pounder-bearing streams of Russia (100–200 km) and Argentina (382 km) are shorter and of glacial origin (Savvaitova et al. 2000; Pascual et al. 2001). The Klamath River is located at latitude 42°N, whereas the half-pounder-bearing streams of Russia and Argentina are located at 57°N and 50°S, respectively. At northern latitudes amphidromy is a common migratory pattern among salmonids. Species of *Salvelinus* from northern coastal streams frequently overwinter in freshwater for reasons other than spawning (Smith and Slaney 1980; Klements et al. 2003, and sources therein). Though Coastal Cutthroat Trout from southern populations display amphidromy (Trotter 1989; Johnson et al. 1999), it is

not necessarily a common pattern among northern California–southern Oregon salmonids.

Why half-pounders exist in some steelhead populations but not others is a question that warrants further attention. In the meantime, we presume that the half-pounder life history developed as a risk-spreading tactic in the face of atypical ocean and (or) inland conditions. If the benefits of the ocean contingent life history consistently outweighed the costs of the ocean contingent life history, steelhead from the lower Klamath River basin would, like steelhead from across the range of the species, remain at sea in the year of initial ocean entry. That a half-pounder life history exists suggests that environmental conditions (i.e., those inland or off the coast) in the northern California–southern Oregon area are not so predictable. In sum, we suggest that the half-pounder life history is a geographically unique basket in which steelhead can put their eggs in the face of uncertainty.

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