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ARTICLE

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.

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 southern 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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