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[Article]

Overwintering Distribution, Behavior, and Survival of Adult Summer Steelhead: Variability among Columbia River Populations

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Abstract.—Unlike most anadromous salmonids, summer steelhead *Oncorhynchus mykiss* overwinter in rivers rather than the ocean for 6–10 months prior to spring spawning. Overwintering in rivers may make summer steelhead more vulnerable to harvest and other mortality sources than are other anadromous populations, but there has been little systematic study of this life history strategy. Here, we used a large-scale radiotelemetry study to examine the overwintering behaviors and distributions of 26 summer steelhead stocks within the regulated lower Columbia–Snake River hydrosystem. Over 6 years, we monitored 5,939 fish, of which 3,399 successfully reached spawning tributaries or the upper Columbia River basin and were assigned to specific populations. An estimated 12.4% of fish that reached spawning areas overwintered at least partially within the hydrosystem (annual estimates = 6.8–19.6%), while the remainder overwintered in tributaries. Across all populations, later-arriving fish were more likely to overwinter in the hydrosystem; overwintering percentages ranged from less than 1% for fish tagged in June to over 40% for those tagged in October. Proportionately more interior-basin steelhead (Clearwater, Salmon, and Snake River metapopulations) overwintered in the hydrosystem than did fish from lower-river populations. Steelhead were distributed in mixed-stock assemblages throughout the hydrosystem during winter, usually in reservoirs closest to their home rivers but also in nonnatal tributaries. Overwintering fish moved upstream and downstream between reaches in all months; a nadir occurred in early January and peak egress into spawning tributaries was in March. The estimated survival to tributaries was higher for fish that overwintered in the hydrosystem (82%) than for fish that did not (62%); this difference was largely attributable to low winter harvest rates. Our results suggest that large main-stem habitats, including reservoirs, may be widely used by overwintering summer steelhead. The complex migration behaviors of steelhead indicate both the potential for adaptation and possible susceptibility to future river environment changes.

The life history strategy of summer steelhead *Oncorhynchus mykiss* (anadromous rainbow trout) is unique among anadromous Pacific salmonids in that returning adults enter freshwater from spring through late fall, overwinter, and then spawn during the subsequent spring (Busby et al. 1996; Quinn 2005). Extended river residence prior to spawning (up to 11 months: Busby et al. 1996) is thought to be an adaptation to long-term environmental conditions in migration corridors and on spawning grounds. Robards and Quinn (2002), for example, hypothesized that seasonal temperature or discharge barriers historically prevented summer-run fish from reaching spawning sites during the season in which they began reproductive migrations. Many interior summer steelhead stocks also migrate from several hundred to more than 1,500 km to reach high-elevation spawning tributaries, and early migration may allow fish to move long distances and achieve large elevation gains that would be impossible at low winter and spring temperatures (Brett 1995; Trudel et al. 2004).

The approximate current geographic center of steelhead distribution in the eastern Pacific is the Columbia River basin (Brannon et al. 2004; Augerot 2005). Annual runs of more than 500,000 steelhead were estimated to have returned to the Columbia River near the end of the 19th century (Chapman 1986), but a variety of well-documented human activities decimated populations during the 20th century (National Research Council 1996; Lichatowich 2001; McClure et al. 2003). Several Columbia River steelhead populations were listed as threatened under the U.S. Endangered Species Act (ESA) in 1997–1999, including all interior-basin summer-run fish (National Marine Fisheries Service 1997; Good et al. 2005). These include mid- and upper-Columbia River populations as well as Snake River steelhead, which have among the longest inland steelhead migrations in the world (Busby et al. 1996). Since receiving ESA listing, some Columbia River steelhead populations have increased in size through hatchery supplementation, conservation efforts, harvest reform, and—in recent years—improved

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