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Status Review of West Coast Steelhead from Washington, Idaho, Oregon, and California

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"Among these fishermen one occasionally hears more or less protracted discussions as to whether the fish are trout or steelheads, whether they belong to the same species as the larger steelheads which enter the river, whether they differ from the smaller stream trout, whether they differ from the steelheads of other rivers, what is a steelhead anyway..." (Snyder 1925, p. 50).

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Steelhead Life History and Ecology

Oncorhynchus mykiss exhibit perhaps the most complex suite of life history traits of any species of Pacific salmonid. They can be anadromous or freshwater resident (and under some circumstances, apparently yield offspring of the opposite form). Resident forms are usually called rainbow, or redband, trout. Those that are anadromous can spend up to 7 years in fresh water prior to smoltification, and then spend up to 3 years in salt water prior to first spawning. The half-pounder life history type in southern Oregon and northern California spends only 2 to 4 months in salt water after smoltification, then returns to fresh water and outmigrates to sea again the following spring without spawning. Another life history variation is the ability of this species to spawn more than once (iteroparity), whereas all other species of *Oncorhynchus*, except *O. clarki*, spawn once and then die (semelparity).

Migration and Spawn Timing

The most widespread run type of steelhead is the winter (ocean-maturing) steelhead. Winter steelhead occur in essentially all coastal rivers of Washington, Oregon, and California, south to Malibu Creek. Summer (stream-maturing) steelhead, including spring and fall steelhead in southern Oregon and northern California, are less common; for example, on the Oregon coast only the Rogue, Umpqua, and Siletz Rivers have natural populations of summer steelhead. Inland steelhead of the Columbia River Basin, however, are essentially all stream-maturing steelhead; as discussed earlier, these inland steelhead are referred to in terms of A-run and B-run.

Available information for natural populations of steelhead (Table 3) reveals considerable overlap in migration and spawn timing between populations of the same run type. Moreover, there is a high degree of overlap in spawn timing between populations regardless of run type. California steelhead generally spawn earlier than those in areas to the north; both summer and winter steelhead in California generally begin spawning in December, whereas most populations in Washington begin spawning in February or March. Relatively little information on spawn timing is available for Oregon and Idaho steelhead populations. Among inland steelhead, Columbia River populations from tributaries upstream of the Yakima River spawn later than most downstream populations.

Ageing

Steelhead exhibit great variation in smolt age and ocean age both within and between populations, but there are some trends.

Smolt age—Smolt age discussed here is based on scale and otolith data from adult steelhead. The emphasis on adult steelhead is based on the assumption that fish surviving to spawning age are expressing the successful and adaptive life history strategy for steelhead in a given geographical location. Steelhead from British Columbia and Alaska most frequently smolt after 3 years in fresh water (Withler 1966, Narver 1969, Sanders 1985). In most other populations for which there are data, the modal smolt age is 2 years (Table 4). Hatchery conditions usually allow steelhead to smolt in 1 year; this difference is often used by

Table 3. Migration (shaded), spawn (s), and peak spawn (P) timing for selected populations of steelhead. Run types of steelhead are indicated by (O) = ocean-maturing and (S) = stream-maturing.

Location / Population (run type) — **Months:**	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J
Alaska																		
Karluk River (S)																		
Anchor River (S)																		
Situk River (S)											P	P						
Situk River (O)																		
Sitkoh Crek (O)																		
Karta River (O)																		
Washington (Puget Sound)																		
Nooksack River (O)													s	s	s	P	s	
Samish River (O)													s	s	P	s		
SKAGIT RIVER BASIN																		
Skagit River (O)														s	s	P	s	
Sauk River (S)															s	s		
Cascade River (S)												s	s	s	s			
STILLAGUAMISH RIVER BASIN																		
Stillaguamish River (O)														s	s	P	s	
Deer Creek (S)															s	s		
S. Fork Stillaguamish River (S)												s	s	s	s			

Table 3. Migration and spawn timing for selected steelhead populations. Continued.

Location Population (run type) — Months:	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J
SNOHOMISH RIVER BASIN																		
Snohomish River (O)														s	P	s	s	
N. Fork Skykomish River (S)																		
Lake Washington (O)																		
Green River (O)														s	P	P	s	
Puyallup River (O)														s	P	P	s	
Nisqually River (O)														s	P	P	s	
Deschutes River (O)												s	P	s	s			
South Sound Inlets (O)													s	P	P			
Tahuya River (O)													s	s	P	s		
Skokomish River (O)													s	s	P	s	s	
Dewatto River (O)													s	s	P	s		
Discovery Bay (O)													s	s	P	s	s	
Dungeness River (O)														s	s	P	s	
Morse Creek (O)													s	s	P	s	s	
Pysht River (O)													s	s	P	s	s	
Hoko River (O)													s	s	P	s	s	

Table 3. Migration and spawn timing for selected steelhead populations. Continued.

Location Population (run type)	Months:	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J
Washington (coastal)																			
Quillayute River (O)														s	s	P	P	s	
Quillayute River (S)																			
Hoh River (O)														s	s	P	P	s	
Hoh River (S)																			
Queets River (O)														s	s	P	P	s	
Queets River (S)																			
Quinault River (O)														s	s	P	P	s	
Quinault River (S)																			
Moclips River (O)													s	s	s	P	P	s	
Copalis River (O)														s	s	s	s	s	
Humptulips River (O)														s	s	P	P	s	
Humptulips River (S)																			
Hoquiam River (O)														s	s	P	P	s	
Wishkah River (O)														s	s	P	P	s	
Wynoochee River (O)														s	s	P	P	s	
Satsop River (O)														s	s	P	P	s	
Chehalis River (O)														s	s	P	P	s	

Table 3. Migration and spawn timing for selected steelhead populations. Continued.

Location / Population (run type) — **Months:**	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J
Skookumchuck River (O)													s	s	P	P	s	
Willapa Bay (O)													s	s	P	P		
Columbia River Basin																		
FRESHWATER ENTRY (S)																		
Grays River, Washington (O)														s	s	s	s	
Elochoman River, Washington (O)														s	P	P	s	
Mill Creek, Washington (O)														s	P	P	s	
Abernathy Creek, Washington (O)														s	P	P	s	
Germany Creek, Washington (O)														s	P	P	s	
Cowlitz River, Washington (O)														s	s	s	s	
Toutle River, Washington (O)														s	P	P	s	
Coweeman River, Washington (O)														s	s	s	s	
Kalama River, Washington (O)														s	P	P	s	
Kalama River, Washington (S)												s	s	s	s			
Lewis River, Washington (S)														s	s	s	s	
Willamette River, Oregon (O)															s	P	s	
Clackamas River, Oregon (O)															s	P	P	
Washougal River, Washington (S)														s	s	s	s	
Wind River, Washington (S)														s	s	s		

Table 3. Migration and spawn timing for selected steelhead populations. Continued.

Location Population (run type) **Months:**	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J
White Salmon River, Washington (S)														s	s	s		
Klickitat River, Washington (S)														s	s	s		
Fifteenmile Creek, Oregon (O)														s	s			
Deschutes River, Oregon (S)													s	s	s	s		
John Day River, Oregon (S)														s	s	s		
Rock Creek, Oregon (S)														s	s	s		
Walla Walla River, Washington (S)														s	s	s		
Touchet River, Washington (S)														s	P	P		
Yakima River, Washington (S)													s	s	P	s		
Wenatchee River, Washington (S)														s	s	P	s	s
Entiat River, Washington (S)														s	s	P	s	s
Methow River, Washington (S)														s	s	s	s	s
Okanogan River, Washington (S)														s	s	s	s	s
Snake River Basin																		
"A"-run freshwater entry (S)																		
"B"-run freshwater entry (S)																		
Tucannon River (S)														s	P	P		
Asotin Creek (S)														s	P	P		
Grande Ronde River (S)														s	s	s		

Table 3. Migration and spawn timing for selected steelhead populations. Continued.

Location Population (run type)	**Months:** F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J
Oregon (coastal)																		
Yaquina River (O)											s	s	s	s	s			
Rogue River (S)												P	P	s	s			
California																		
Smith River (O)												s	P	s	s			
Smith River (S)											s	P	s					
Klamath River (O)											s	s	s	P	s	s		
Klamath River (S)											s	P	s					
Trinity River (O)										s	P	P	P	P	s			
Trinity River (S)											s	P	s					
Redwood Creek (O)											s	P	s	s				
Redwood Creek (S)																		
Mad River (O)												s	P	P	s			
Mad River (S)																		
Jacoby Creek (O)											s	s	P	P	s			
Freshwater Creek (O)											s	s	P	P	s			
Eel River (O)										s	s	P	P	s	s			
Eel River (S)											s	P	s	s				
Pudding Creek (O)											s	P	P	s				

Table 3. Migration and spawn timing for selected steelhead populations. Continued.

Location / Population (run type)	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J
Casper Creek (O)													s	P	s			
Gualala River (O)												s	P	s				
Russian River (O)											s	P	P	P	s	s		
SACRAMENTO RIVER BASIN																		
early run (O)											s	s	P					
late run (O)												s	P	P	s	s		
American River (O)											s	P	P	s	s	s		
Feather River (O)										s	s	P	P	s	s	s	s	
Mokelumne River (O)											s	s	P	s	s			
San Gregorio Creek (O)											s	s	P	s				
Waddell Creek (O)											s	P	P	P	s	s		
Scott Creek (O)											s	P	P	P	s	s		
San Lorenzo River (O)											s	s	P	s				
Carmel River (O)												s	P	P	s			
Santa Ynez River (O)											s	s	P	P	s	s	s	
Ventura River (O)												s	P	P	s	s	s	
Santa Clara River (O)											s	s	P	P	s	s	s	
Malibu Creek (O)												s	P	P	s			

biologists to distinguish hatchery and wild steelhead. There appears to be an increase in the frequency of naturally produced 1-year-old smolts in the southern portion of the steelhead range (Table 4). Withler (1966) suggested that there may be a latitudinal cline in steelhead smolt age; however, Titus et al. (in press) found no statistical evidence for a latitudinal cline in steelhead smolt age from California to British Columbia.

Ocean age—North American steelhead most commonly spend 2 years (*2-ocean*) in the ocean before entering fresh water to spawn (Table 5). Populations in Oregon and California have higher frequencies of age-1-ocean steelhead than populations to the north, but age-2-ocean steelhead generally remains dominant. Withler (1966) and Titus et al. (in press) found that ocean age at spawning (and mean adult length) increased with increasing latitude.

Total age—For most steelhead populations, total age at maturity can be estimated by adding the smolt age and saltwater age. However, summer steelhead (especially in the Columbia River Basin) enter fresh water up to a year prior to spawning, and that year is generally not accounted for in the saltwater age designation; for example, a 2-ocean steelhead from the Yakima River may actually have 3 years between smolting and spawning. Table 6 shows the most common life history patterns expressed by North American steelhead from several river basins. Most steelhead in Alaska and British Columbia are 3/2 (smolt age/ocean age) and have a total age of 5 years at first spawning. For coastal steelhead in Washington, Oregon, and northern California, the modal total age at maturity is 4 years (2/2). Central and southern California steelhead appear to spend less time in the ocean, and they are dominated by 3-year-old (2/1) spawners. Complete life history data for southern California steelhead are lacking; however, it appears that it is common for these fish to smolt in 1 year (CDFG 1995). If they only have one ocean year, as neighboring populations to the north do, then adults may be spawning as 2-year-olds (1/1) in this region.

Determining total age at maturity for inland steelhead of the Columbia River Basin is complicated by variations in reporting methods. Generally, these fish spend a year in fresh water prior to spawning and this is not included in the age designation. Therefore, by adding 1 year after freshwater entry (indicated here as $^{+1}$), most Columbia River inland steelhead are 4 years old at maturity ($2/1^{+1}$). An exception is the Klickitat River; if these steelhead also spend a year in fresh water before spawning, they are dominated by 5-year-old spawners ($2/2^{+1}$). Most of the available age data for Snake River steelhead are based on length frequency; smolt age is often assumed or not reported. The data that are available from scales show a high degree of variability in age structure, from 4-year-old spawners ($2/1^{+1}$) in the Clearwater River (Whitt 1954) to 7 year-old spawners ($3/3^{+1}$) in the South Fork Salmon River (BPA 1992).

Repeat Spawning

As noted above, most species of *Oncorhynchus* die after spawning, whereas *O. mykiss* may spawn more than once. The frequency of multiple spawnings is variable both within and among populations (Table 7). For North American steelhead populations north of Oregon, repeat spawning is relatively uncommon, and more than two spawning migrations is rare. In Oregon and California, the frequency of two spawning migrations is higher, but more than two spawning migrations is still unusual. The largest number of spawning migrations for which we found data was five, from the Siuslaw River, Oregon (Bali 1959). Iteroparous steelhead are predominately female.

Resident Fish

Although we have defined steelhead as anadromous *O. mykiss*, there are areas where the separation between rainbow or redband trout and steelhead is obscured. In areas where anthropogenic barriers have isolated populations of *O. mykiss*, these landlocked populations could conceivably residualize[5] and, therefore, continue to exist in the nonanadromous form. Similarly, the mouths of some rivers in Oregon and California close seasonally, forming lagoons (during droughts, these rivers may remain closed for extended periods of time—even years). Again, landlocked *O. mykiss* in these systems could residualize. In some inland populations, growth rate can cause *O. mykiss* to residualize (Mullan et al. 1992); this apparently involves both fish that grow too quickly and those that grow too slowly.

Steelhead Genetics

Previous Studies of Population Genetic Structure

Protein electrophoresis—Allendorf (1975) first distinguished two major groups of *O. mykiss* in Washington, Oregon, and Idaho, separated geographically by the Cascade Crest; he termed these groups inland and coastal. These two groups have large and consistent differences in allele frequency that apply to both anadromous and resident forms. Subsequent studies have supported this finding (Utter and Allendorf 1977, Okazaki 1984, Schreck et al. 1986, Reisenbichler et al. 1992), and similar differences have been identified between *O. mykiss* from the interior and coastal regions of British Columbia (Huzyk and Tsuyuki 1974, Parkinson 1984).

Several genetic studies since the mid-1970s have used protein electrophoresis to examine population structure in coastal or inland *O. mykiss*. Allozyme studies of coastal Oregon steelhead have been reported by Hatch (1990) and Reisenbichler et al. (1992). Hatch (1990) surveyed 13 protein-coding loci in steelhead from 12 hatcheries and 26 coastal rivers or tributaries in Oregon. He found evidence for a north-south cline in allele frequencies in 5 of the 13 enzyme systems analyzed, but only in river basins larger than 350 km^2. Hatch also reported that “the area south of the Coos River was marked by sharp transition in four enzymes...” (p. 17) and that “the pattern of several alleles ending their detectable Oregon

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[5] Residual *O. mykiss* are those that have an anadromous lineage but are themelves nonanadromous; the term was first proposed by Ricker (1938) in describing life-history variations in *O. nerka*. The change in life history may be the result of a physical or physiological barrier to migration (e.g., a dam, or slow growth that precludes smoltification).