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The Migratory Timing of Adult Summer-Run Steelhead in the Columbia River over Six Decades of Environmental Change

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Abstract.—Anadromous fishes achieve most of their lifetime growth at sea before returning to spawn in freshwater. However, populations of some species enter freshwater many months before spawning, apparently compromising growth opportunities at sea to access spawning grounds in conjunction with specific seasonal patterns of flow and temperature along the migratory route. The nutritional benefits of overwintering in the ocean may also be outweighed by a relatively dormant winter in colder river habitats. Modification of the thermal and hydrologic regimes of rivers (such as the Columbia River during the 20th century) might be expected to affect the abundance and life history patterns of such populations. This study reviews information on the migratory timing, abundance, and composition (wild versus hatchery) of summer-run (upriver) populations of steelhead *Oncorhynchus mykiss* in the Columbia River basin with reference to environmental changes. Despite pronounced changes in the river's environment, the late summer migration-spring spawning persists as an overall pattern as it passes Bonneville Dam (the lowest on the Columbia River). However, the historic summer run's distinct bimodality (with early and late components) has gradually become unimodal. Upriver, other complex changes have taken place in migration timing: it now occurs earlier through some reaches of the river and periods of time, reflecting both the uneven physical changes over time and the complex behavior and population structure of steelhead. We were unable, therefore, to isolate the causal mechanisms or disentangle natural from anthropogenic influences. However, our research suggests that the change in the migration pattern for summer-run steelhead reflects a response to the challenges presented by a changing environment (temperature and flow) to genetically controlled life history patterns, the relative abundance of component populations, and the relative proportion of populations derived from hatchery production (which lately [1984–1999] accounted for an average 74% of the early run and 85% of the late run).

Anadromous fishes, including many salmonids, are spawned in freshwater but achieve the majority of their lifetime growth at sea before they return to freshwater to spawn (McDowall 1988; Groot and Margolis 1991). Anadromy seems to be an evolutionary adaptation to take advantage of the security of freshwater for breeding and the relative productivity of marine environments for growth typical at higher latitudes (Northcote 1979; Miller and Brannon 1982; Gross et al. 1988). Migration is a cost that anadromous fishes must pay to take advantage of these discrete habitats. Despite the advantages that large body size conveys for egg production and competition on spawning grounds, some salmonids leave the ocean many months before spawning, apparently forgoing prime feeding opportunities at sea in the summer; these include some populations of chinook salmon *Oncorhynchus tshawytscha* (Healey 1991), Atlantic salmon *Salmo salar* (Went 1964; Shearer 1990), and steelhead (anadromous rainbow trout) *O. mykiss* (Busby et al. 1996; Thorpe 1998).

Summer-run steelhead (also known as river-maturing steelhead; Busby et al. 1996) enter freshwater from May to October in a sexually immature condition, remain in rivers all winter (often more than 6 months), and spawn the following spring. In contrast, winter-run (also known as ocean-maturing) steelhead enter freshwater from November to April with well-developed gonads and spawn shortly afterwards. Summer steelhead constitute most of the inland steelhead of the Columbia River basin. There they spawn in snowmelt-dominated, relatively dry mountainous regions,

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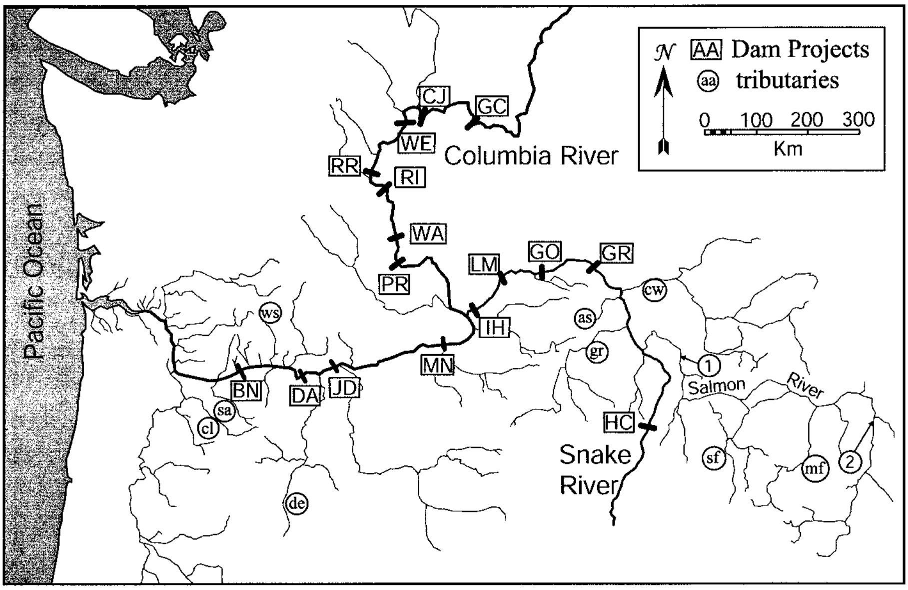

FIGURE 1.—Map of the Columbia River system showing the main-stem dams within the recent range of steelhead; BN = Bonneville, DA = The Dalles, JD = John Day, MN = McNary, PR = Priest Rapids, WA = Wanapum, RI = Rock Island, RR = Rocky Reach, WE = Wells, CJ = Chief Joseph, GC = Grand Coulee, IH = Ice Harbor, LM = Lower Monumental, GO = Little Goose, GR = Lower Granite, and HC = Hells Canyon. Tributaries referred to in the text are indicated as follows: cl = Clackamas River, sa = Sandy River, ws = White Salmon River, de = Deschutes River, as = Asotin Creek, gr = Grande Ronde River, cw = Clearwater River, and sf and mf = the South and Middle forks of the Salmon River. Numbers 1 and 2 on the Salmon River indicate U.S. Geological Survey hydrological station numbers 13317000 and 13302500, respectively.

with very different patterns of flow and temperature than the much wetter, rainfall-dominated coastal river systems (Busby et al. 1996). Summer steelhead in the Columbia River basin, particularly the Snake River subbasin, have traditionally been referred to as either A- or B-run by local biologists and managers. These designations are based primarily on a bimodal distribution of upstream migration by adults, noticeable at Bonneville Dam, but also correspond to differences in body size. A-run steelhead pass Bonneville Dam (river km [rkm] 234, measuring from the mouth of the Columbia River ; Figure 1) from June to August (by conventional definition, up to 26 August), whereas the B-run fish pass the dam from late August to October (Busby et al. 1996). A-run fish tend to spend one full year at sea and average about 75–100 mm smaller (fork length [FL]) than the older and larger B-run fish (Busby et al. 1996). B-run steelhead are thought to spawn only in certain tributaries of the Snake River: the Clearwater River, and the Middle and South Forks of the Salmon River (Figure 1). The A-run or early-run fish appear to spawn throughout the mid- to upper Columbia and Snake River systems.

The 20th century saw dramatic anthropogenic changes in the physical environment of the Columbia River, the largest river in western North America and prime habitat for many salmonid species. The construction of a complex system of dams has greatly affected the river's flow and temperature regimes (Figure 1; Quinn and Adams 1996; Quinn et al. 1997). Changes in flow regime were designed to modify the river's natural snowmelt-dominated hydrograph to allow generation of hydroelectric power, storing water in late spring for release in winter when natural flows were low (Ebel et al. 1989). Changes in the thermal regime may have resulted from a combination of natural and human factors. In concert with the development of hydroelectric projects, habitat degradation, interactions with hatchery fish, and fisheries, these changes have caused declines in the wild portion of many salmonid populations (including steelhead) within the basin (National Research Council 1996). Declines in these steelhead populations led the National Marine Fisheries Service to list several steelhead Evolutionarily Significant Units (ESUs; see Waples 1991) on the Columbia and Snake rivers as threatened or endangered under the U.S. Endangered Species Act (ESA; 62 FR 43937). However, despite the application of the ESA, surprisingly little information has been published on the behavior and ecology of adult steelhead within these river systems. Notably, the patterns of migratory timing and spawning have not been carefully examined, despite the fact that timing contributes substantially to the apparent population structure in the basin.

The timing of upriver migration and spawning in salmonids is primarily an adaptive response to long-term average conditions rather than a proximate response to prevailing conditions. Genetic control over the timing of upstream migration or spawning has been established for many salmonid species, including rainbow trout (Siitonen and Gall 1989), Chinook salmon (Quinn et al. 2000), Atlantic salmon (Hansen and Jonsson 1991), and pink salmon *O. gorbuscha* (Smoker et al. 1998). However, environmental factors, notably flow and temperature, also affect entry into freshwater and upstream migration rate of salmonids by stimulating or retarding movement (Major and Mighell 1967; Banks 1969; Gilhousen 1980, 1990; Jensen et al. 1989; Smith et al. 1994; Quinn and Adams 1996; Trépanier et al. 1996; Quinn et al. 1997). In the Columbia River, sockeye salmon *O. nerka* historically entered the river before water temperatures reached their peak and when flows were decreasing. The increased peak temperatures and earlier warming of the river have been associated with earlier migration by sockeye salmon (Quinn and Adams 1996).

We hypothesize that some combination of temperature and flow regime prevents stream-maturing adult steelhead from reaching their spawning grounds shortly before spawning, so they overwinter and mature in freshwater rather that at sea. Most summer-run steelhead seem to pass Bonneville Dam after the summer peak of temperatures and so might be predicted to migrate later in recent years because of the longer warm period in the lower river. However, our ability to understand the patterns of timing that seem so central to the biology of steelhead is complicated by several factors. First, hatchery-produced steelhead have been selected for early return and maturation date and now differ distinctly from wild fish (Ayerst 1977; Leider et al. 1984). Second, the environmental conditions in many rivers and especially in the Columbia River system have been changed so greatly that they may now constitute a new regime of natural selection as well as an altered range of proximate stimuli for migration. Third, the relative abundance (and productivity) of populations, each with its characteristic timing pattern, may have changed and so altered the overall pattern of the species.

It is important to distinguish changes in abundance that affect the entire summer steelhead population from those that affect only steelhead from specific drainages. Within the Columbia River basin, centennial-scale changes in overall steelhead abundance are largely attributable to anthropogenic perturbations (Chapman 1986). Runs were estimated to have peaked around 1892–1896, numbering up to 554,000. Subsequently, runs decreased in response to overfishing and environmental degradation, including lost or degraded spawning habitat and mortality of juveniles migrating downstream through as many as nine mainstem dams and reservoirs en route to the ocean. Since 1975, improved passage through the dam complexes for both adults and juveniles (Raymond 1988) may have contributed to the strong returns of steelhead in the late 1970s. However, these returns coincided with an increase in some summer-run steelhead populations below the dams (e.g., the Sandy and Clackamas rivers; T. Murtagh and others, Oregon Department of Fish and Wildlife, unpublished data) and in some steelhead in the Fraser River system, British Columbia (Smith 1999). These increases also coincided with a regime shift in oceanic climate during the mid-1970s (Francis et al. 1998). The abundance of the early run has shown declines since the mid-1980s, as has that of the late run since 1992.

The primary objective of this study was to describe the patterns of migratory timing of summer-run steelhead above Bonneville Dam (the lowest point of count) in the Columbia River basin over the past decades. We recognize that the complex population structure of steelhead (e.g., wild versus hatchery) and responses to physical changes in the river, and perhaps at sea as well, make it difficult to unravel the relationships between environmental factors and steelhead runs. However, the six decades of steelhead counts at Bonneville Dam and associated environmental data in the river provide an important historical record that should be used to better understand this species at risk. Specifically, we assessed how the traditional management descriptors of the steelhead migration (e.g., A- and B-runs) relate to present patterns in the Columbia and Snake rivers, and determined how these two components of the run have changed over the past 60 years. From the hypothesis that steelhead would avoid very warm water, we predicted that the runs

TABLE 1.—Dam projects on the Columbia River for which steelhead passage data were used for this study.

Project	Operator	Date of completion	Year of first fish count	Usual hours of counting	River km[a]
Bonneville	Corps of Engineers	1938	1938	0400–2000	234
The Dalles	Corps of Engineers	1957	1957	0500–2100	306
John Day	Corps of Engineers	1967	1968	0500–2100	345
McNary	Corps of Engineers	1953	1953	0400–2000	467
Ice Harbor	Corps of Engineers	1961	1961	0400–2000	537
Priest Rapids	Grant County Public Utility District	1959	1963	0500–2100[b]	639
Rock Island	Chelan County Public Utility District	1933	1933	0500–2100[b]	726

[a] Measured from the mouth of the Columbia River, including Ice Harbor Dam on the Snake River.
[b] Since 1992, counting has been over 24 h by video.

would be getting progressively later because warmer peak temperatures and longer warm period in the summer might select for later migrants or might stimulate migrants to wait in the lower river longer before moving upstream in fall. Alternatively, earlier timing might indicate the effects of the earlier-migrating hatchery fish accounting for a larger proportion of the fish. We also examined timing patterns at a series of dams to investigate the progression of migration upriver, which could not be revealed by counts at a single location.

Methods

Sources of data.—The U.S. Army Corps of Engineers (USACE) annual fish passage reports (1938–1999; Table 1) provided the data on temperature, flow, and counts of total steelhead (wild and hatchery) passing dams on the main-stem Columbia River (Bonneville, The Dalles, John Day, and McNary dams) and Snake River (Ice Harbor Dam). Summer-run steelhead populations spawn in some tributaries of the Columbia River below Bonneville Dam (the lowermost dam on the main stem of the river), but their timing within the main stem has not been assessed in a similar systematic manner so we did not examine them. Data for Priest Rapids and Rock Island dams, on the Columbia River above its confluence with the Snake River, were obtained from their respective operators, the Public Utility Districts (PUDs) of Grant and Chelan counties. The U.S. Geological Survey provided river flow and temperature data independent of dam projects (at The Dalles and Salmon River; Figure 1). The 1938–1949 annual passage reports were not published, but we copied data from the original manuscripts stored at Bonneville Power Station Library, which recorded counts at fish ladders, the primary route of passage past dams. However, some steelhead may use the dam's navigation locks while vessels are transiting, and some may ''recycle,'' that is, passing up the ladders, falling back down the spillways, and then again climbing the ladders to be counted more than once. We assumed these sources of error were likely to be offsetting. The data accounted for breaks taken by personnel during regular counting hours (Table 1) by simple expansion. Data collected before 1960 at Rock Island were irregular and have been omitted from our analysis, and no data were collected there between 1968 and 1972.

Since 1995 at Bonneville and 1993 at Ice Harbor, 24-h video monitoring has allowed assessment of nighttime passage of steelhead. Nighttime passage from 1 June until 31 October averaged 7.3% and 10.0% of the daytime counts at Bonneville and Ice Harbor, respectively (USACE 1995–1999). These results indicate that the daytime count period (16 h) adequately represents the 24-h biological patterns. The proportion of nighttime passage (<10%) appears consistent with other migratory species in the Columbia River (e.g., sockeye salmon and American shad *Alosa sapidissima*; Quinn and Adams 1996). For consistency, and because these corrections might not necessarily apply in past years, we did not adjust the counts for nighttime passage. We also did not adjust the data from Priest Rapids and Rock Island, which during the 1990s conducted 24-h video surveillance, rather than 16-h visual counts.

Data analysis.—Sizeable portions of several populations (especially in the Snake River) remain below mainstream dams during the winter and resume migration the following spring (Howell et al. 1985). Given this overwintering behavior, we have used ''fish years,'' defined as 1 June–31 May, rather than calendar years for depicting migratory timing. These arbitrary dates have been used previously and represent low points on composite graphs for migration above Bonneville Dam (Busby et al. 1996; Figure 2). We recognize (as have others using this method) that some overlap occurs

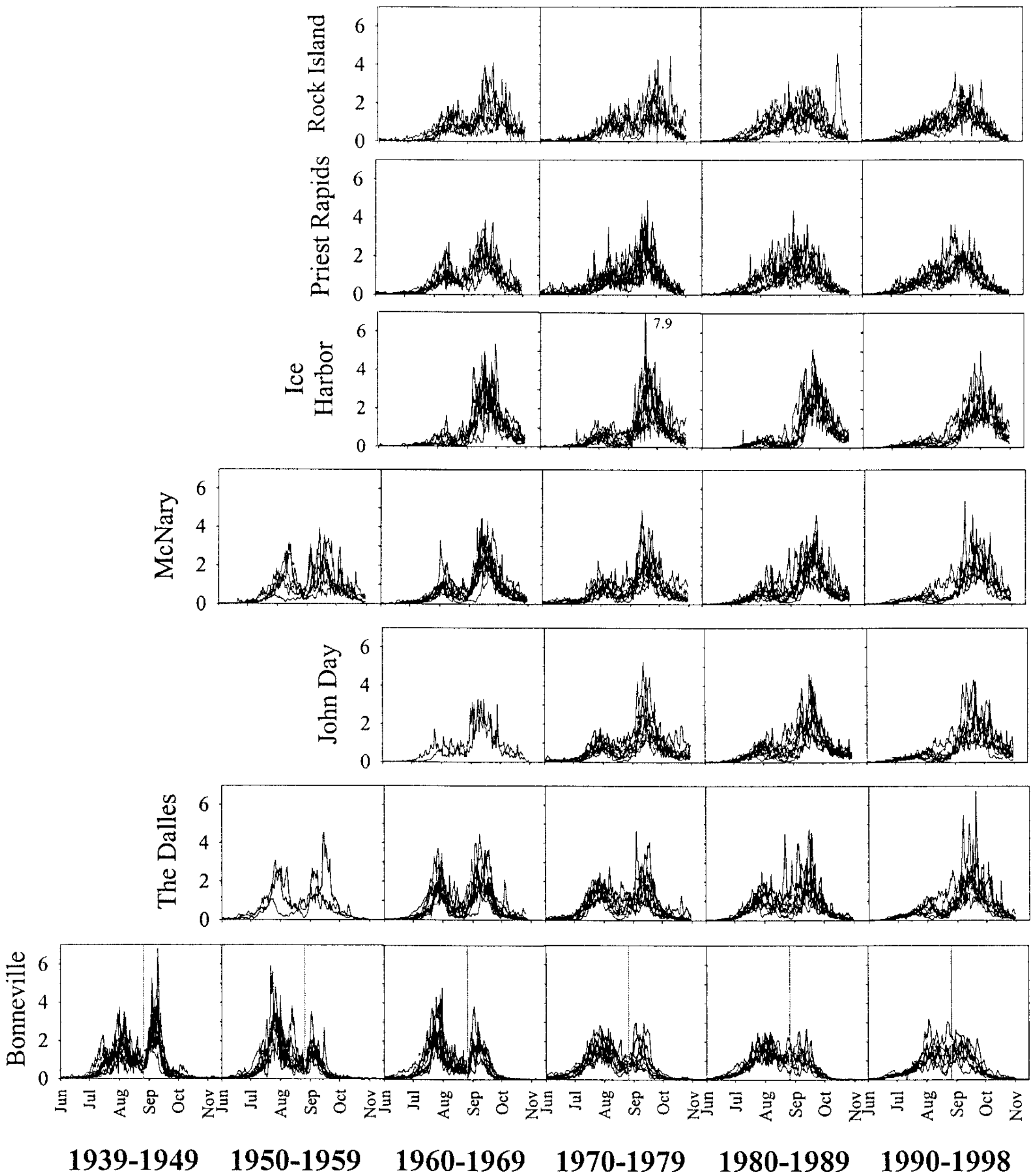

FIGURE 2.—Percent daily runs, grouped by decade, for the main-stem dams with salmonid counts on the Columbia River and Ice Harbor Dam on the Snake River. Graphs are plotted from 1 June to 31 October except those for Bonneville Dam, which are plotted until 15 November. Each decadal graph consists of 10 (annual) lines, each consisting of about 150 data-days (16 h per day). The black vertical lines on the Bonneville plots represent the arbitrary split between early and late runs.

in individual years. That is, fish counted in June might be either very late for one year or very early for the next.

The focus of this study was the seasonal pattern of summer migration of steelhead over multiple decades. To compare timing, we portrayed daily counts as a percent of the summer run, starting 1 June and for consistency ending 15 November at Bonneville or 31 October at all others dams (date of the last count for many years). Visual inspection

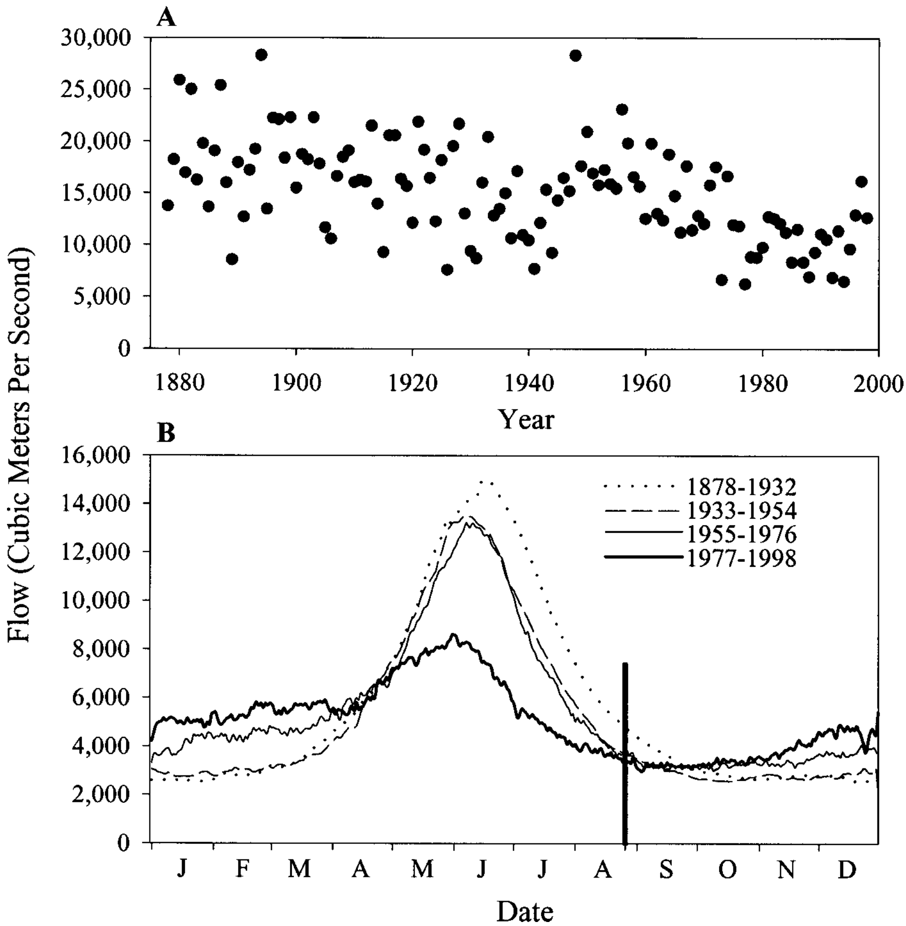

FIGURE 3.—Effect of reservoir operation on Columbia River flows at The Dalles, Oregon. Data are from the U.S. Geological Survey national information system files for station number 14105700. Panel **(A)** shows annual peak flows, panel **(B)** the monthly patterns of flow for the predam period (before 1932) and three subsequent 21-year periods. The vertical line in **(B)** indicates an arbitrary split between early and late runs.

of the dam passage plots indicated that these dates largely encompassed the summer migration. By converting numbers to percent we could compare migration patterns for different years irrespective of run size. Several researchers have used the date of ‘‘50% of the run’’ (i.e., the median day, when half the total number of migrants had passed the dam) to indicate the peak of migratory runs (e.g., Leggett and Whitney 1972; Quinn and Adams 1996). However, the migration of summer-run steelhead in the Columbia River system has two distinct peaks, precluding the value of such analysis. Therefore, we plotted running 7-d means of daily percent passage. From these smoothed data, we estimated the 7-d average peak days for the early and late runs in each year. In years and at dams with no early or late run, only the single peak date was calculated. We described modes as early and late run to prevent confusion with the A- and B-run designators, which also reflect age and size of migrants.

Results

Physical Environment

The increased number of storage dams in the upper Columbia and Snake rivers over the past 60 years has greatly increased control of the water flow. By storing water, naturally high summer flows from snowmelt are reduced, and low winter flows are increased (Figure 3), allowing for relatively stable power production throughout the year. Flows at Rock Island Dam increased from 1933 until the early 1950s, but Bonneville, McNary, and

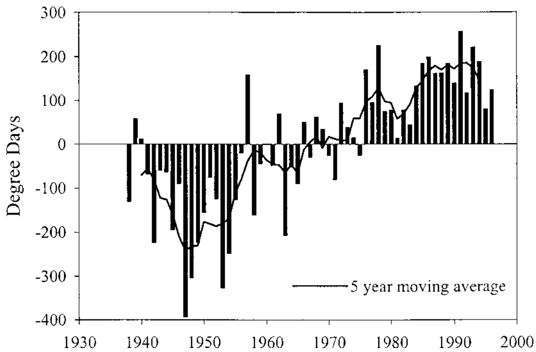

FIGURE 4.—Variation in summer temperatures at Bonneville Dam. Bars represent degree days, defined as the annual sum of daily deviations (°C) from the 1938–1998 daily temperature averages. The line represents a smoothed version of this data, obtained by using a 5-year moving average.

Rock Island dams all experienced substantial decreases in summer flow since the 1950s.

At Bonneville, decreased summer flow (and variability of flow; Figure 3) since 1950 has paralleled increasing summer water temperatures (Figure 4). Furthermore, spring warming has begun earlier and fall cooling has begun later for the section of the Columbia River from Bonneville to McNary Dam. Farther upriver, mean summer temperatures (for 1975–1994) at Priest Rapids have not changed significantly (although peak temperatures are about 3°C warmer now), whereas mean temperatures at Rock Island decreased until the 1960s and have since steadily increased (Quinn et al. 1997). Mean temperatures did not change since the 1960s at Ice Harbor on the Snake River, although fall cooling has begun later. Spatially, temperatures above dam projects (e.g., in the Salmon River) showed a similar pattern of seasonal warming to peak temperatures in late July/early August. However, during the latter part of migration from September on, fish in the Salmon River experienced markedly cooler temperatures than in the mainstem Columbia River, and subsequent winter temperatures have been much cooler than those at Bonneville (Figure 5). Not all of these changes in the environmental characteristics of the upper Columbia River system should be attributed to dam projects. For example, the pattern of generally high peak flows between 1940 and 1960 at Bonneville Dam was similar to conditions above dam projects (e.g., Salmon River; Figure 6).

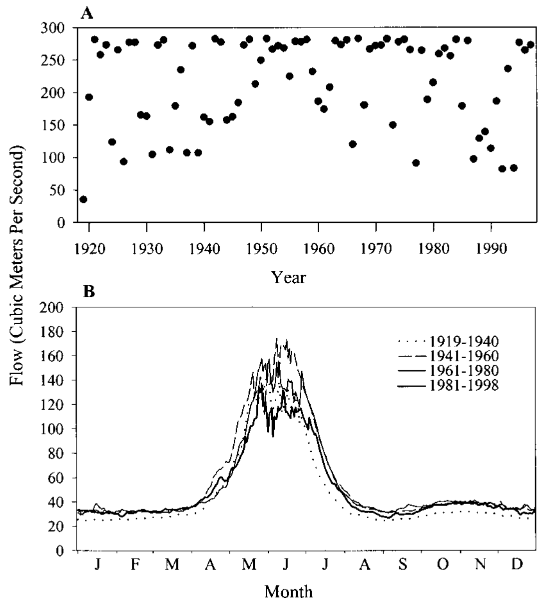

FIGURE 6.—Flow patterns observed above dam projects on the Salmon River at USGS hydrological station 13302500 (see Figure 1). Panel **(A)** shows annual peak flows, panel **(B)** the monthly patterns of flow over four equal time periods since the inception of flow monitoring.

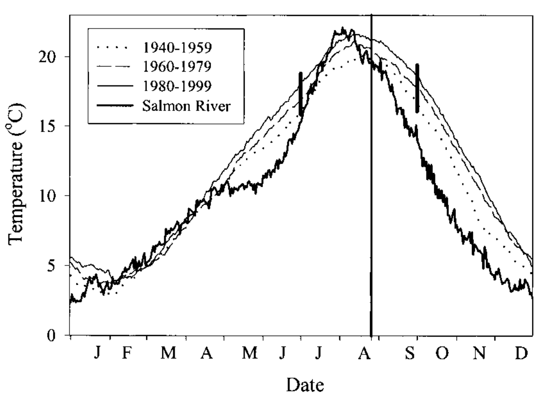

FIGURE 5.—Monthly pattern of water temperatures at Bonneville Dam over three equal periods since construction. Shown for comparison are the 1969–1977 data from the Salmon River (USGS hydrological station 13317000) above the dam projects. The thick vertical black bars depict the general boundaries of the summer-run steelhead migration period; the thin vertical line indicates the cutoff point between the arbitrarily defined early and late runs.

Steelhead Abundance

The abundance of returning adult summer-run steelhead (hatchery and wild) counted at Bonneville Dam (Figure 7) revealed an increase in the number of early-run fish during the early 1950s;

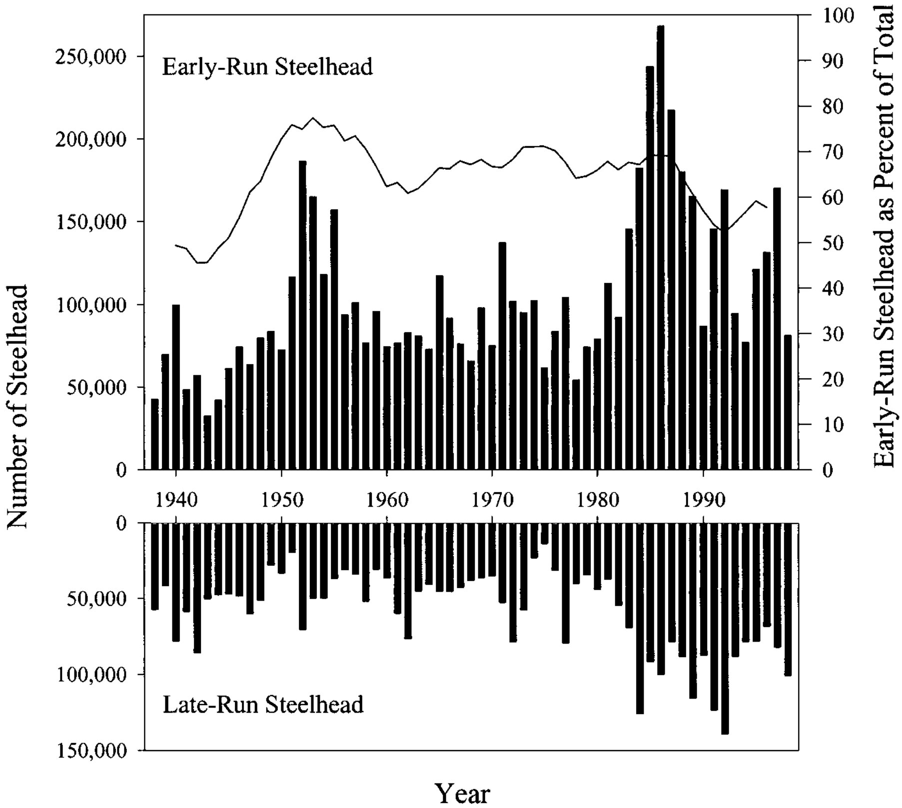

FIGURE 7.—Abundance of the early and late portions of the summer steelhead run passing Bonneville Dam. The line in the upper panel is a 5-year running average of the proportion of the run defined as early (i.e., passing Bonneville Dam on or before 26 August).

the most noticeable increase, however, was from the late 1970s until the mid-1980s. This pattern in abundance was also observed below Bonneville Dam for summer-run steelhead on the Sandy and Clackamas rivers (Murtagh and others, unpublished data). This apparent resurgence of steelhead largely reflects hatchery production and probably masks the scarcity of wild steelhead. For example, wild steelhead have been counted separately at Bonneville Dam since 1984 (ODFW/WDFW 1995; USACE 1993–1999), during which time they have averaged only 26% of the early and 15% of the late portion of the summer run (Figure 8).

The relative proportions of the early and late segments of the summer run have varied over the past six decades. At the start of the 1940s, approximately 50% of the steelhead in the early run passed Bonneville Dam between 1 June and 31 October. The annual proportion increased to a maximum of 86% in 1951 (Figure 7 portrays a 5-year running average) and has returned to about 50% of the run at present (Figure 7).

Temporal and Spatial Patterns of Upriver Steelhead Migration Timing

Data we reviewed from all dams, including those above the confluence with the Snake River, provided clear evidence of the bimodal summer steelhead run before the 1970s (Figure 2), except that the early run in the Snake River was very small. Therefore, neither the early nor late mode is unique to either river, as is graphically suggested by the traditional A/B descriptors. The bimodal run pattern at all the dams has greatly diminished over time, although counts at dams between Bonneville and the confluence with the Snake River are still noticeably bimodal, despite the fact that the early run is much smaller than the late run. During the 1940s as much as 7% of the annual total run passed Bonneville Dam on a single day, but the currently more protracted run has a daily run passage of less than one half this. Analysis of peak run days for each of the early and late modes (Figure 9; Table 2) indicated clear temporal and

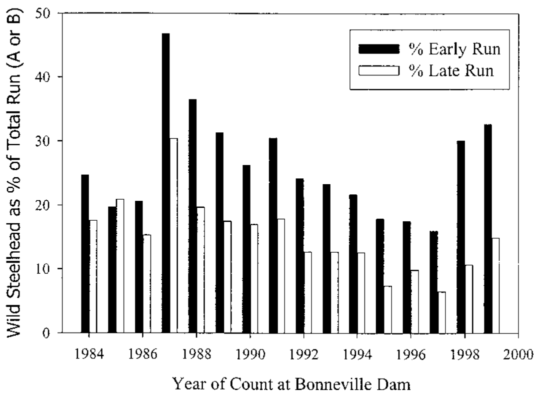

FIGURE 8.—Proportions of wild steelhead in the early and late runs passing Bonneville Dam for the years 1984–1999.

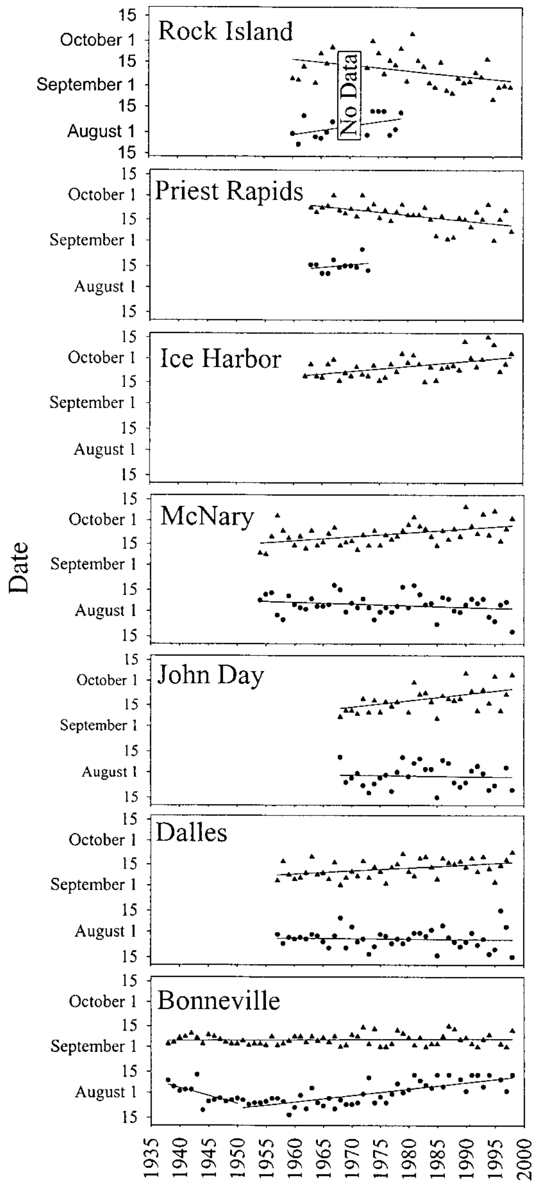

FIGURE 9.—Peak migration dates of early (circles) and late (triangles) steelhead passing main-stem dams in the Columbia River system. Trend lines are linear regressions for early- and late-run peak migration dates over time (see Table 2 for parameters).

spatial trends. Bonneville data, the longest record, showed progressively earlier migration by the early run until about 1950. Subsequently, in association with decreasing peak flows (Figure 3) and warming average temperatures (Figure 4), this run has shifted and is now about 21 d later than in 1950. In contrast, the late run has shown no long-term change (mean peak passage date = 6 September, SD = 4 d), despite some interannual variation. Consequently, the timing of the early and late runs is now closer together at Bonneville Dam. In years when the river's discharge was greater, steelhead of the early run tended to migrate past Bonneville Dam significantly earlier than in years of lower discharge (r^2 = 0.29, P < 0.001). No significant relationship was detected with water temperature or between the timing of the late run and either temperature or flow.

Early runs at all dams above Bonneville did not show the same trend towards later migration since the 1950s (Figure 9). Indeed, the runs have become slightly earlier below the confluence of the Snake River (The Dalles, John Day, and McNary dams). However, the late run, which was temporally stable at Bonneville, has become later over the period of record for the three dams below Priest Rapids Dam, resulting in a greater separation of the timing of the early and late runs (though the early run is diminished in relative abundance). In contrast, the late run is becoming earlier farther up the Columbia River at Priest Rapids and Rock Island. The late run to the Snake River (i.e., Ice Harbor Dam) has been getting later (Figure 9), and the early run is too small (Figure 2) for estimation of reliable trends.

Discussion

It is difficult to explain all of the changes in patterns of steelhead migration associated with the environmental conditions 60 years ago compared with those of the Columbia River basin as it is today. The migratory patterns expressed are an amalgam of the timing of many distinct wild and

TABLE 2.—Linear regression results for peak adult summer-run steelhead passage past main-stem dams on the Columbia River against year. Results are included for both the early and late portions of the runs.

Dam	Run	Data period	Slope	Intercept[a]	r^2	P-value
Bonneville	Early	1938–1949	−1.071	2,143	0.403	0.020
	Early	1950–1998	0.438	−803	0.596	<0.001
	Late	1938–1998	0.021	57.5	0.010	0.452
The Dalles	Early	1957–1998	−0.027	109.5	0.003	0.743
	Late		0.207	−304.7	0.180	0.005
John Day	Early	1968–1998	−0.048	155.0	0.003	0.768
	Late		0.429	−739.7	0.157	0.027
McNary	Early	1953–1998	−0.109	280.6	0.045	0.160
	Late		0.270	−420.8	0.234	<0.001
Ice Harbor[b]	Mode	1961–1998	0.334	−544.0	0.248	0.002
Priest Rapids[c]	Late	1963–1998	−0.386	874.6	0.309	<0.001
Rock Island	Early	1960–1979	0.567	−1,036.0	0.241	0.075
	Late	1960–1998	−0.383	875.5	0.166	0.019

[a] Date was plotted starting with 1 June.
[b] There was only a single mode for the migration at this dam.
[c] There were insufficient data for the early run to calculate a regression.

hatchery populations produced from a range of locations in this huge basin—not merely two runs, one early and one late. Nevertheless, summer steelhead passing the lowermost dam (Bonneville) revealed two stanzas of change in timing. The early run became earlier until shortly after 1950, after which it has gotten later. This trend is consistent with the prediction that changes in timing would correlate with changes in river flows and temperatures (see Figures 3 and 4). By migrating progressively later in lower flows and after the peak temperatures, steelhead mirror the progressively earlier timing in sockeye salmon that migrate before the peak temperatures. Furthermore, migration timing for both these species responded at the inflection point for thermal changes at about 1950 (Quinn and Adams 1996).

Steelhead migration above Bonneville Dam revealed very complex patterns; the early and late runs displayed different trends over different periods of time and over different reaches of the river. Populations may migrate in distinct stages, holding in specific reaches between periods of upstream migration. Moreover, the reservoirs provide lacustrine habitat that would not have been present in the unregulated river. For example, steelhead bound for the Umatilla River pass Bonneville Dam by July but may not pass John Day Dam until the following March (Howell et al. 1985). Furthermore, different parts of the same spawning stock may migrate in a disjunct manner. Steelhead from the Grande Ronde and Asotin drainages pass through the lower Snake River drainage in two parts, the first peaking in mid- to late September and the second in April to early May (Howell et al. 1985). Our results indicated that early- and late-run steelhead behaved differently in the reservoir above Bonneville Dam, thus resulting in more marked timing differences at The Dalles and John Day dams. These results are consistent with the common impression that steelhead commonly hold in tributaries of the Columbia between Bonneville and John Day dams such as the White Salmon or Deschutes rivers (L. Beck, U.S. Army Corps of Engineers, personal communication). The ‘‘holding’’ between dams, nonlinear migration rates, and complex population structure prevented calculation of travel rates upriver (as had been done for sockeye salmon in the Columbia River by Quinn et al. 1997).

Disorientation of adults as they negotiate the ladders around specific dams, particularly as engineered changes to facilitate passage have taken place, may affect observed migration timing. For example, Leman and Paulik (1966) demonstrated a strong relationship between the ability of salmonids to locate fish passes and manipulation of spillway gates at Rock Island Dam. Improved salmon passage was also apparent at Priest Rapids Dam after improvements were made to facilitate passage there in 1977. Modifications at both of these dams may have resulted in earlier passage. Conversely, dams themselves may have improved historical passage through some sections of the Columbia River such as Celilo Falls, which was inundated in 1957 by construction of The Dalles Dam. Despite these and other difficulties in determining the precise relationships between changing environmental conditions and steelhead responses over more than six decades in a huge basin, nevertheless some distinct patterns are apparent and we attempt to explain them in the remainder of this discussion.

The population dynamics of steelhead in the Pacific Northwest appear to be associated with large-scale climatic changes affecting the eastern rim of the North Pacific (Welch et al. 2000). However, the temporal and spatial changes in Columbia River summer steelhead migration patterns (notably, the marked changes in the 1950s) are more probably attributable to changes in the riverine environment. Summer steelhead enter the river in late summer, long in advance of spawning, hold in the deeper and comparatively warm main stem during the winter period of cold water and low flows, and ascend tributaries to spawn in spring. Our working hypothesis is that the fish have made an evolutionary compromise between the need to feed at sea to store energy for migration and reproduction, and the need to arrive at distant spawning locations in the late winter and spring. This compromise is comparable to the tradeoffs made by other salmonids returning to freshwater long in advance of spawning. If the fish are large, the forgone feeding opportunities at sea may not incrementally affect size much. The challenge is to explain the long-term riverine conditions that have favored such a life history pattern and to estimate the effects of river modification.

Flow and Temperature

Flow patterns were most strongly related to steelhead migration timing. Flow is frequently cited as stimulating or controlling the rate of upstream migration by salmon. Jensen et al. (1989) indicated that adult Atlantic salmon in Norway could migrate only when river flows were below a certain level so that waterfalls could be negotiated. Banks (1969) also indicated that Atlantic salmon prefer moderate rather than high or low flows. Low flows may slow passage of salmon (Banks 1969; Liscom et al. 1985), and observers at Bonneville Dam observed less hesitation at flashboards during periods of greater flow (April 11, 1939; USACE 1939). It is difficult to understand the detailed hydraulics of passage around rapids and falls that no longer exist, such as at Celilo Falls, but steelhead migration may well have evolved to get upriver at appropriate flows for passage at such sites.

Historically, summer steelhead in the Columbia River migrated in summer and early fall (July–October), at least 1 month after the summer peaks in river flow (Figures 2 and 3). Not only has the main-stem Columbia River seen decreased summer peak flows and increased winter flows, but also the peak now occurs somewhat earlier (Figure 3). At Bonneville Dam, early-run steelhead (which migrate in higher flows than late-run fish; Figure 3) migrated earlier as peak flows increased into the 1950s, but since then, when peak flows have decreased, their migrations have come progressively later (Figure 9). These patterns of change suggest that avoidance of higher flows is not the primary factor determining timing.

Mean flow alone does not appear to explain the early migration of steelhead into the river system some 8 months before spawning. Flows in the early spring are similar to those in the fall at the time of the summer-run migration. Steelhead could leave the ocean in February or March, swim to their spawning grounds, and arrive at the same time as those that overwintered in freshwater. However, this possibility neglects the role of low temperature in swimming performance and also the variation in river flow. Migration would occur in water temperatures much cooler than those found in the fall (Figure 5). Furthermore, summer steelhead that arrive early in the fall, when flows are still too high to negotiate an area of difficult passage, can wait and ascend later. If they migrated in spring and encountered excessively high flows (which would probably only get higher), then they might be unable to reach spawning grounds in time. In addition, the interaction between flow and passage may also be most critical in the spring at the spawning grounds, particularly those at high elevations where freezing and beaver dams might slow flows to impassable amounts. In these cases, steelhead appear to wait for increased flow rather than a specific temperature cue (Spence 1981; Lough 1983).

Throughout the last 60 years, both the early and late portions of the summer steelhead run have migrated past Bonneville Dam close to or after annual peak summer temperatures. During the cooler temperatures of the 1950s, early-run steelhead migrated earlier but began migrating progressively later during the subsequent warming years. The early run has been ascending Bonneville Dam later in the summer (roughly mid-August rather than early August), but their thermal regime is much the same. Elson (1969) reported increased migration intensity for Atlantic salmon with water temperatures within 5–6°C of their upper lethal temperature limit (about 30°C). Steelhead may favor warm temperatures for their initial upstream migration, before holding in the cooler water above Bonneville Dam (USACE 1955; L.

Beck, personal communication) to reduce energy loss (as for spring chinook salmon; Berman and Quinn 1991). The timing of steelhead migration has apparently not evolved to minimize temperatures in the lower river, because they can migrate later in the fall, and the shifts in migration timing with temperature suggest a relatively warm preferred temperature for initiating ascent. In contrast, Columbia River sockeye salmon seem constrained to migrate before the peak temperatures, when flows are decreasing (Quinn and Adams 1996).

In addition to summer peak temperatures, cold winter temperatures may affect the evolution of migratory timing in steelhead. Thompson et al. (1958) reported that steelhead in the Snake River drainage stopped migrating when temperatures went below 3°C and resumed movement in the spring when theysurpassed 4°C. Summer steelhead in the Skeena and Chilcotin rivers of interior British Columbia also moved little during winter (Spence 1981; Lough 1983). Swimming performance decreases at very low temperatures (Brett 1995), and tributaries at high elevations may partially freeze in winter, reducing flow to impassable amounts until the spring. Therefore, by overwintering in freshwater, steelhead lose some growth opportunities at sea in late summer. However, winter growth at sea is slight (Burgner et al. 1992), and the overwintering steelhead are near the spawning grounds when spring temperatures increase and the timing is suitable for reproduction. The cold, low-flow conditions in deep pools could facilitate an effectively dormant winter condition in a predator-free environment, minimizing mortality and loss of energy reserves, which may not be possible at sea. The surprisingly stable timing of the late run at Bonneville Dam, particularly in comparison with the early run, suggests that late-run steelhead may not experience stressful conditions or conditions that are substantially altered from their biological perspective, resulting in no change.

Fisheries

Although the impacts of dams on smolt survival may affect the early- and late-summer steelhead runs equally, those from fishing may be selective on specific Columbia River populations or runs, as has been observed for Skeena River, British Columbia, populations (W. E. Chudyk and D. W. Narver, British Columbia Fish and Wildlife Branch, unpublished data). Columbia River steelhead have been caught in three main fisheries (ODFW/WDFW 1995): a non-Indian commercial fishery (which was closed in 1975), a treaty Indian fishery, and a non-Indian recreational fishery. Early regulations (since 1909) closed the commercial fishing season from 25 August to 10 September. These regulations have largely persisted in the commercial fishery below Bonneville Dam and until 1968 in areas above Bonneville Dam. Since 1968, fishing has occurred between these dates in the fishery above Bonneville Dam. As a result of the 25 August to 10 September closure below Bonneville, harvests of steelhead have presumably focused more on the peaks of the early and late runs rather than on the dip in abundance between these runs (Figure 2). Heavy fishing on the peaks of the two runs is consistent with the more generalized distribution that is currently observed at Bonneville.

Hatcheries

Summer steelhead are more abundant now than in the 1940s (Figure 7) and include wild and hatchery fish. The proportion of wild steelhead in 1938 is unknown, but only four hatcheries existed above Bonneville Dam on the Columbia and Snake rivers before 1940 (Busby et al. 1996). In contrast, since the 1970s, the main stems and at least 19 tributaries have been receiving steelhead from 18 different hatchery sources (Busby et al. 1996). The destruction of available habitat and proliferation of hatcheries have decreased wild stocks to less than a quarter of the current runs. The high extent of genetic control over migration and spawning timing in salmonids (e.g., Quinn et al. 2000) means that selection in hatcheries can quickly affect the timing of steelhead migration. Some steelhead hatcheries deliberately selected for earlier spawning date (Ayerst 1977), and other hatchery programs (e.g., Columbia River coho salmon; Flagg et al. 1995) also resulted in earlier spawning. However, the delay in steelhead migration is not consistent with this effect and so is probably related to environmental conditions, especially the altered flow and thermal regimes.

Conclusion

Over the past six decades, the pattern of summer-run steelhead migrations in the Columbia River has changed. Primarily, the marked bimodal migration of summer-run steelhead has become much less obvious. The two components of this bimodality (early and late) have responded differently over time. At Bonneville Dam, the timing of the early run has correlated to the changing physical environment of the river, with runs becoming progressively later in conjunction with warmer temperatures and reduced flows. In contrast, the late-run pattern has changed remarkably little, probably as a result of less stressful conditions, or conditions less different from the biological perspective of the fish. Complex migration habits (such as holding for long periods) have made evaluation of patterns at upstream dams equivocal. Variation in the relative abundances of the steelhead component populations as a result of fishing and the wild: hatchery ratio has probably influenced the patterns of steelhead migration as well.

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