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Artificial Selection and Environmental Change: Countervailing Factors Affecting the Timing of Spawning by Coho and Chinook Salmon

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Abstract.—Spawning date is a crucial life history trait in fishes, linking parents to their offspring, and it is highly heritable in salmonid fishes. We examined the spawning dates of coho salmon *Oncorhynchus kisutch* and chinook salmon *O. tshawytscha* at the University of Washington (UW) Hatchery for trends over time. We then compared the spawning date patterns with the changing thermal regime of the Lake Washington basin and the spawning patterns of conspecifics at two nearby hatcheries. The mean spawning dates of both species have become earlier over the period of record at the UW Hatchery (since the 1950s for chinook salmon and the 1960s for coho salmon), apparently because of selection in the hatchery. Countering hatchery selection for earlier spawning are the increasingly warmer temperatures experienced by salmon migrating in freshwater to, and holding at, the hatchery. Spawning takes place even earlier at the Soos Creek Hatchery, the primary ancestral source of the UW populations, and at the Issaquah Creek Hatchery. Both species of salmon have experienced marked shifts towards earlier spawning at Soos Creek and Issaquah Creek hatcheries despite the expectation that warmer water would lead to later spawning. Thus, inadvertent selection at all three hatcheries appears to have resulted in progressively earlier spawning, overcoming selection from countervailing temperature trends.

Compared with most other fishes, salmonids produce large eggs with a protracted incubation period. Spawning date is the primary factor controlling the date when offspring emerge from the gravel in the spring, and it is an adaptation to the prevailing ecological conditions during incubation and emergence, influencing juvenile survival and growth (Brannon 1987; Brännäs 1995; Webb and McLay 1996; Einum and Fleming 2000; Quinn et al. 2000). The timing of adult migration and reproduction differs greatly among salmonid populations, but within populations, timing varies only slightly among years (Ricker 1972; Brannon 1987; Groot and Margolis 1991). Timing of migration and reproduction is largely under genetic control in a variety of salmonid species (Siitonen and Gall 1989; Hansen and Jonsson 1991; Su et al. 1997; Smoker et al. 1998; Quinn et al. 2000). Dates of migration and spawning seem to reflect selection for adult passage (Quinn and Adams 1996) and incubation of embryos (Brannon 1987), and timing diverges in populations transplanted outside their range (Quinn et al. 2000).

The high heritability of spawning date means that it can be affected rapidly by artificial selection in hatcheries as well as by natural selection. Practices in hatcheries can directly select for the timing of maturation if early-maturing fish are spawned and late-maturing fish are discarded. Indirect selection for early maturation may also occur if the progeny of late-maturing fish are (1) culled as too small, (2) cannot compete in the hatchery with the larger progeny of early spawners, (3) fail during the smolt transformation process, or (4) have lower survival rates at sea. Deliberate selection for spawning date in steelhead *Oncorhynchus mykiss* in Washington resulted in markedly earlier spawning, allowing hatchery staff to grow the fish to smolt size in 1 year rather than 2 years (Ayerst 1977; Crawford 1979). Progressively earlier spawning has also been documented in lower Columbia River coho salmon *O. kisutch* populations (Flagg et al. 1995).

The timing of salmon migration and reproduction is thus affected by environmental conditions and artificial selection, but how might the fish re-

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spond to a combination of these pressures? To investigate this question, we examined detailed data, collected since the 1950s, on coho salmon and chinook salmon *O. tshawytscha* spawning at the University of Washington (UW) Hatchery. Our goals were to (1) test the hypothesis that the timing of spawning by coho and chinook salmon has become earlier since the 1950s, (2) determine whether timing patterns are consistent with salmon avoidance of warm temperatures during spawning, and (3) compare the spawning timing of chinook and coho salmon populations at the UW Hatchery with that at the Issaquah Creek Hatchery in the same basin and that at the Soos Creek Hatchery, the primary ancestral source of the UW populations.

Methods

History of the UW Hatchery.—In the early 1930s, Dr. Lauren Donaldson conducted preliminary experiments on the growth and culture of salmon and trout at the UW campus (Hines 1976). After World War II, Dr. Donaldson designed and constructed a salmon and trout hatchery on the UW campus to facilitate his research on radiation ecology. The first chinook salmon were released in 1949, and the UW Hatchery ponds and fishway became operational in 1950 (Allen 1959). The salmon migrate about 8 km to the hatchery from Puget Sound (Figure 1) via the Lake Washington Ship Canal, opened in 1917 to link Lake Washington and Lake Union to Puget Sound by way of the Hiram Chittenden Locks. The hatchery was modified in 1960, when a bulkhead was built, turning a cove in Portage Bay into a holding pond for returning adult salmon. The facility has otherwise been structurally similar since its construction.

The chinook and coho salmon populations were primarily derived from the Green River system (Soos Creek Hatchery; Figure 1), though exchanges with other populations took place over the years. The Soos Creek Hatchery itself has had exchanges with many other populations, chiefly, but not exclusively, within Puget Sound. The UW Hatchery successfully produced chinook salmon since the 1950s. The population is ocean-type (i.e., migrate to sea in their first year of life; Healey 1991), characteristic of most lowland Puget Sound hatchery and wild populations (Myers et al. 1998). Coho salmon were also introduced in the 1950s (Donaldson and Allen 1958) from Soos Creek Hatchery. However, the UW Hatchery's main water source is the Lake Washington Ship Canal, which drains the epilimnion of Lake Washington, and the water

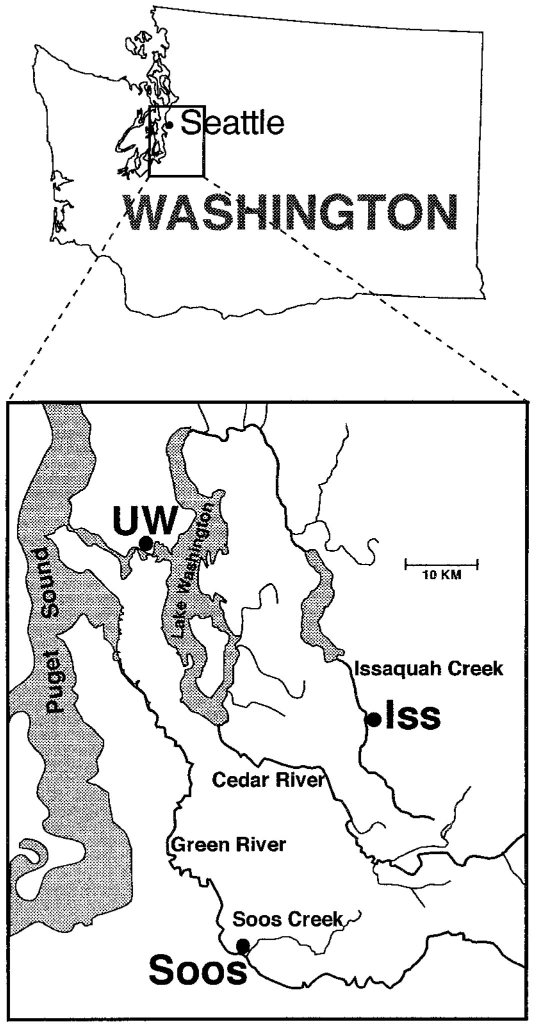

FIGURE 1.—Map of central Puget Sound, showing the locations of the University of Washington (UW), Issaquah Creek (Iss), and Soos Creek (Soos) hatcheries.

temperatures in the summer often prove stressful or lethal for juvenile coho salmon. In the 1950s and early 1960s, the numbers of returning coho salmon were low and variable. In 1967, additional smolts were brought from Soos Creek Hatchery and released, and their returns in 1969 represent the present lineage of this species at the UW Hatchery. To avoid problems associated with the UW Hatchery's warm summer temperatures, coho salmon are reared on an elevated temperature regime during incubation and are fed heavily so they can reach a suitable size for smolt transformation in their first spring (Feldmann 1974; Donaldson and Brannon 1976; Brannon et al. 1982), unlike the region's typical wild and hatchery populations, which rear in freshwater for a full year before migrating to sea (Sandercock 1991; Weitkamp et al. 1995).

Dr. Donaldson practiced selective breeding of rainbow trout and chinook salmon, especially in the early years (1953–1972) of the UW Hatchery. The objectives of the breeding program were to select chinook salmon for early maturation age, rapid growth, high fecundity, and high survival rate of eggs, fry, and fingerlings (Donaldson and Menasveta 1961; Donaldson 1970; Hines 1976). There may have been some selection against late-maturing salmon by culling their progeny (E. L. Brannon, personal recollection), but there are no specific records to demonstrate this. No control lines were kept, and the strength of the selection and its effects on any of the traits are unclear. Since Dr. Donaldson's retirement in 1972, there has been no directed selection on spawning date and only episodic selection experiments with other traits, such as age at maturity. The Soos Creek and Issaquah Creek hatcheries have been operated by the Washington Department of Fisheries (now Department of Fish and Wildlife) since 1901 and 1936, respectively.

Data collection and analysis.—Since the late 1950s, all salmon returning to the UW Hatchery were checked for ripeness and, when ripe, were killed, identified, measured for fork length, and weighed; the date was also recorded, along with any marks or other pertinent data. The spawning operation was typically conducted on Monday, Wednesday, and Friday of each week, when every fish was identified to species and sex, and checked for ripeness to spawn. Ripe fish were sacrificed and later spawned by extracting the eggs from females and fertilizing them with milt from males. The date of spawning closely represents the date females were fully mature, but males remain ripe over a longer period of time, and surplus males were sometimes killed to thin out the number of salmon being held. Because the date when males were killed is not a reliable indicator of maturation date, we only analyzed data for females. Females not fully mature when killed for spawning were excluded from the analyses, as were females that died in the pond prior to being spawned. Females that spawned all or some of their eggs in the gravel-lined hatchery pond before being killed were used for analysis because their spawning date would have been no more than a day or two from the date recorded.

The data were examined for trends over the years in spawning date of the UW Hatchery coho and chinook salmon, and spawning timing patterns of UW Hatchery populations were compared with those of conspecifics from the Issaquah Creek and Soos Creek hatcheries. For the latter analysis, we obtained data from 1960 to 2000 for chinook salmon and from 1942 to 2000 for coho salmon (data from earlier years were not available). Spawning typically took place once or twice weekly at these hatcheries. At Soos Creek and Issaquah Creek hatcheries (unlike the UW Hatchery), not all salmon are spawned and recorded. Salmon in excess of the hatchery's capacity may be killed, and some salmon spawn in the nearby creeks. Thus, the records from those hatcheries reveal trends in timing but are less representative than those at the UW Hatchery, where no natural spawning occurs and where records of all salmon are kept. We calculated the median spawning dates (i.e., date when 50% of the annual total had been spawned) and the mean dates for each year and species to assess possible changes over time. The distributions did not differ from normality. Means and medians showed identical patterns and explained similar amounts of variation, so we conducted all analyses on mean dates.

To compare the spawning date trends with local thermal regimes, we obtained data collected from a limnology station at the surface of Lake Washington since 1972 (T. Edmondson and D. Schindler, University of Washington, Department of Zoology, unpublished data). Both the UW and Issaquah Creek hatchery populations swim through the ship canal, and the Issaquah Creek fish also swim through the lake, so surface temperatures generally represent the thermal regime experienced by these populations. We also obtained data on the temperature regimes of Soos and Issaquah creeks, collected at the hatcheries with minimum–maximum thermometers since 1972. Temperatures recorded daily from 1984 to 2000 were used to characterize the present thermal regimes of these sites. Prior to 1984, only weekly data were available, so we calculated monthly mean temperatures from 1972 to 2000 to assess trends in temperature.

Results

Coho salmon at the UW Hatchery have been spawning progressively earlier, from late November in 1969 to the middle of November at present (Figure 2), with a significant fit to a linear relationship ($P < 0.001$, slope $= -0.31$, $r^2 = 0.22$). The coho salmon spawning dates have not only become earlier but also less variable, as indicated by a linear decrease in the standard deviation of

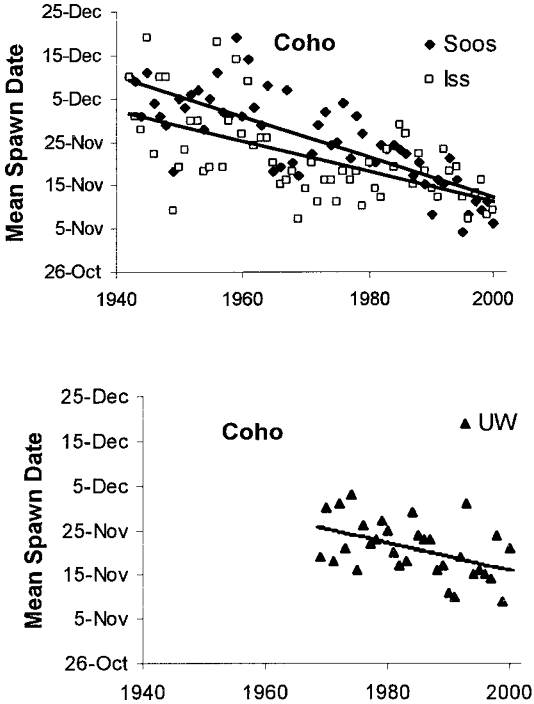

FIGURE 2.—Mean spawning dates of female coho salmon at the Issaquah Creek (Iss) and Soos Creek (Soos) hatcheries (top panel) and at the University of Washington (UW) Hatchery (bottom panel).

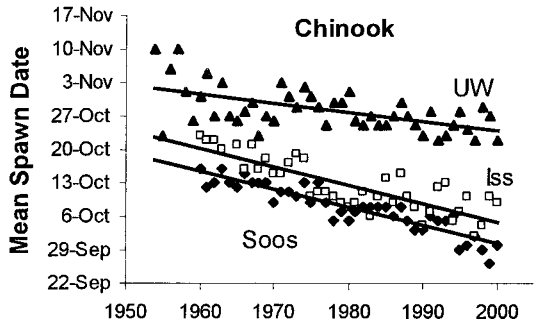

FIGURE 3.—Mean spawning dates of female chinook salmon at the Issaquah Creek (Iss), Soos Creek (Soos), and University of Washington (UW) hatcheries.

the mean spawning date from about 20 d in 1969 to about 12 d in 2000 (P = 0.013, r^2 = 0.19). Chinook salmon at the UW Hatchery spawn earlier in the year than coho salmon, and their mean date has also become earlier from 1954 to 2000 ($P <$ 0.001, slope $= -0.19$, r^2 = 0.33), but the change has been smaller than that seen in the coho salmon (Figure 3). In the first 24 years of data, the peak of the chinook salmon spawning season ranged from late October to mid-November, and in the past 23 years, the spawning season has consistently peaked within the last week of October. The variability in spawning date, as indicated by the standard deviation, has shown no trend over the period of record (r^2 = 0.037). However, this trend is influenced by the first four years of records, when very few (8–34) salmon returned and their spawning dates varied greatly. Since 1958, the variability in spawning date has increased slightly (from about 7.5 to 9 d; $P <$ 0.01, r^2 = 0.15).

Trends towards earlier spawning were detected for both coho and chinook salmon at Issaquah Creek and Soos Creek hatcheries (coho salmon: Issaquah Creek r^2 = 0.36, Soos Creek r^2 = 0.62; Figure 2) (chinook salmon: Issaquah Creek r^2 = 0.68, Soos Creek r^2 = 0.84; Figure 3). The modern UW Hatchery coho salmon population was derived from the Soos Creek population, and the first generation returned in 1969. At that time, the spawning dates of the populations were nearly the same (regressions of spawning date over time for the populations intersect in 1973). However, in the most recent period (1995–2000), the UW coho salmon mean spawning date (18 November) was later than the Soos Creek (8 November) and Issaquah Creek (11 November) mean spawning dates. In contrast, the UW and Soos Creek chinook salmon populations differed in spawning date over the entire period of record (Figure 3), and are several weeks apart at present (mean dates from 1995 to 2000: 30 September at Soos Creek, 8 October at Issaquah Creek, and 26 October at UW). Analysis of the data since 1995 revealed significant (P < 0.001) variation among sites and years, but most of the variation was among sites (analysis of variance [ANOVA] F-values for site comparisons were 2,096.9 for coho salmon and 14,250.8 for chinook salmon, compared with 481.5 for coho salmon and 48.2 for chinook salmon among years). For both species, fish spawned earliest at Soos Creek Hatchery, followed by Issaquah Creek Hatchery and then UW Hatchery.

The Lake Washington surface temperatures peaked in mid-August and commonly exceeded 19°C in summer (21.3°C was the peak average daily temperature; Figure 4, top panel). Linear regression indicated significant increases in the average temperatures for August ($P <$ 0.05), September ($P <$ 0.001), October ($P <$ 0.001), and November ($P <$ 0.05). The mean daily temperature pattern for September is particularly important because it represents the best water temperatures experienced by UW and Issaquah Creek salmon in

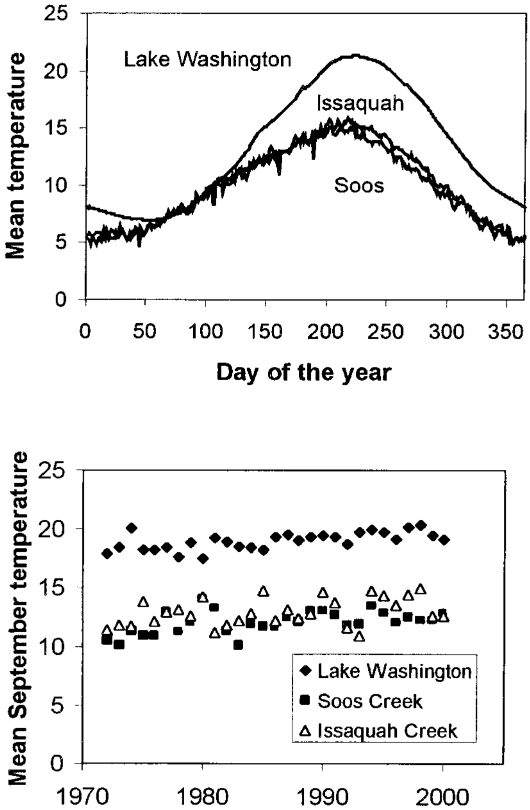

FIGURE 4.—Average surface temperatures (°C) in Lake Washington, Soos Creek Hatchery, and Issaquah Creek Hatchery from 1984 to 2000 (top panel) and average September temperatures from the surface of Lake Washington, Soos Creek Hatchery, and Issaquah Creek Hatchery from 1972 to 2000 (bottom panel).

the final stages of migration and maturation (Figure 4, bottom panel).

To test for association of temperature with salmon spawning date, we calculated water temperature residuals by taking the difference between the observed mean monthly Lake Washington temperature for each year and the monthly temperature estimated from the regression of temperature against year. The UW Hatchery chinook salmon spawning date residuals (i.e., difference between the mean annual spawning date and the date predicted by the overall trend) were positively correlated with the temperature residuals. That is, the salmon tended to spawn later when the water was warmer in September ($P = 0.002$, $r^2 = 0.21$; Figure 5) and October ($P = 0.011$, $r^2 = 0.15$). No correlations were observed with August and November temperature residuals. The UW Hatchery coho salmon spawning date residuals were not corre-

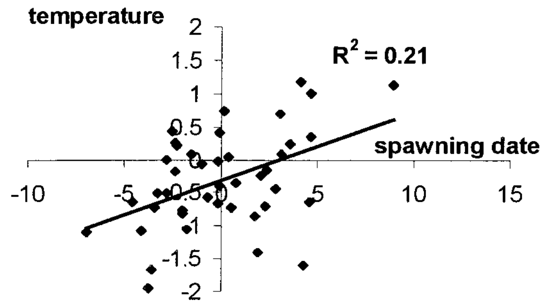

FIGURE 5.—Correlation between the residuals of September Lake Washington water temperature and mean chinook salmon spawning date after eliminating the time trends in the data sets ($N = 42$). Positive residuals correspond to warmer-than-average temperatures and later-than-average spawning dates; see text for details of calculations.

lated with the temperature residuals for any month from August through November ($P > 0.10$ in all cases).

The temperatures at the Issaquah Creek and Soos Creek hatcheries were much cooler throughout the year than the Lake Washington temperatures (Figure 4, top panel). However, Issaquah Creek was significantly warmer than Soos Creek, based on daily temperatures averaged from 1984 to 2000 (Issaquah Creek annual mean = 10.16°C; Soos Creek mean = 9.83°C; paired t-test: $t = 12.82$, $P < 0.001$). The difference between creeks was most pronounced in the summer and declined in fall and winter. Issaquah Creek was warmer than Soos Creek by 1.02°C in September, 0.66°C in October, 0.46°C in November, and 0.31°C in December. As with Lake Washington, an increasing temperature trend was observed in both creeks since 1972 (Issaquah Creek $P = 0.036$, $r^2 = 0.15$; Soos Creek $P = 0.005$, $r^2 = 0.25$; Figure 4, bottom panel).

Discussion

Salmonids have evolved spawning dates that are appropriate for the regimes of temperature and other environmental factors that prevail during incubation (Ricker 1972; Brannon 1987; Murray et al. 1990; Webb and McLay 1996; Quinn et al. 2000). The ocean-type chinook salmon that predominate in the Puget Sound region typically spawn earlier than coho salmon (Weitkamp et al. 1995; Myers et al. 1998), and the same pattern was observed at all three hatcheries. Coho salmon spawn in small streams, where low flow rates and high water temperatures may constrain them from entering or spawning in early fall. Chinook salmon usually spawn in larger rivers, where they are less frequently affected by these conditions. Coho salmon seem to compensate for the later spawning by developing faster at a given temperature than chinook salmon (Murray and McPhail 1988; Murray et al. 1990), and also spend a year in freshwater prior to seaward migration.

Superimposed on these species-specific patterns was the trend towards earlier spawning by both salmon species at all three hatcheries, which has probably resulted from several indirect and direct processes. First, natural selection against early spawning from redd disturbance (e.g., van den Berghe and Gross 1989; McPhee and Quinn 1998) is relaxed in the hatchery because the embryos are protected. Second, early-emerging juveniles are fed and protected in a hatchery, whereas those emerging too early in a stream may encounter limited food and waiting predators, so another form of selection against early spawning is relaxed. Third, juveniles produced by late-spawning females may not reach a suitable size for smolt transformation or marine survival (Holtby et al. 1990), and therefore may be selectively culled at the hatchery or may experience low survival rates after release. This factor may be particularly important for the UW Hatchery coho salmon, which must grow fast enough to make the transition to seawater by the end of their first spring. Offspring of female coho salmon spawning in January and February are unlikely to grow and survive at comparable rates to those of earlier spawners, given this constraint. Early experiments on coho salmon at the UW Hatchery by Feldmann (1974) indicated both higher postrelease survival of progeny from early spawners, and a tendency of the spawning date of progeny to reflect the parental spawning date. However, survival is a complex function of release date as well as of size, so the largest smolts may not always experience the highest survival rates after release (e.g., coho salmon in British Columbia [Bilton et al. 1982] and UW chinook salmon [Whitman 1987]). Moreover, late-emerging fry are fed heavily in hatcheries and may catch up to fry that emerged earlier (Unwin et al. 2000), reducing the advantage of early fry.

In addition to indirect forms of selection for spawning date in hatcheries, direct selection exists as well. Hatchery managers commonly spawn all of the earliest salmon that mature, whereas later-maturing fish may be sacrificed or released into the river when the facility's capacity has been reached. Despite efforts to avoid this practice and spawn representative fish over the whole run, some selection has likely taken place. Given the strong genetic control over migration and maturation date (e.g., Quinn et al. 2000), it is not surprising that hatcheries have advanced the timing of spawning (Flagg et al. 1995; our data). Interestingly, there is evidence that the arrival date (as opposed to spawning date) of chinook salmon at the Soos Creek Hatchery was getting earlier even prior to the years we examined (1944–1965; Miller and Stauffer 1967).

The data not only reveal differences in spawning date between species and trends towards earlier timing at all three hatcheries, but they also show patterns of timing variation among populations. The Soos Creek Hatchery chinook salmon spawned the earliest, followed by Issaquah Creek and then UW chinook salmon. The order of spawning is consistent with the thermal regimes: coolest at Soos Creek Hatchery then Issaquah Creek Hatchery, and warmest at UW Hatchery. The difference in timing among populations was less pronounced in coho salmon. In the early years, coho salmon spawned earlier at Issaquah Creek Hatchery than Soos Creek Hatchery, but the populations converged and are similar at present. Differences between the two species are consistent with the fact that differences in the thermal regimes at Soos and Issaquah creeks were greater in early fall, when chinook salmon spawn, than when coho salmon spawn. The differences in timing among the hatchery populations are noteworthy, given that these are not pure, isolated demes. Rather, exchanges of fish among these and other hatcheries within (and even beyond) Puget Sound have occurred at various times over the years.

The divergence of spawning date, a trait closely linked to fitness, in hatchery populations is an important consideration for genetic and ecological interactions between wild and hatchery-produced salmon (Waples 1991; Utter 1998). The trends in coho salmon spawning timing at UW Hatchery and Soos Creek Hatchery, the primary source population, provide insights into this process. The timing of coho salmon spawning at the two hatcheries was similar in the years when the transplant took place, but at present, the coho salmon spawn later at UW than at Soos Creek. Differences in timing may have resulted from adaptation to the respective thermal regimes (colder at Soos Creek than UW) or from differences in the intensity of selection. In any case, the recent divergence of timing indicates that the two populations are evolving, but at different rates. The similarity in timing in the years when the transplant took place suggests that the UW Hatchery coho salmon population was founded by representative fish from the Soos Creek Hatchery population. In contrast, chinook salmon at the UW and Soos Creek hatcheries differed in timing even in the early 1960s, indicating that either the UW fish rapidly diverged from the Soos Creek population in the years immediately following the transplant, or the salmon used to found the UW population were from the late part of the Soos Creek run.

In addition to selection in hatcheries, changing environmental conditions also select for timing. The migratory timing of sockeye salmon *O. nerka* in the Columbia River indicated both short-term (year-to-year) responses to changing temperature and flow conditions and a long-term trend consistent with genetic adaptation to the river's increased temperatures and reduced flows (Quinn and Adams 1996; Quinn et al. 1997). Lake Washington, Soos Creek, and Issaquah Creek have been getting warmer in the summer and fall over the past three decades, and the warming trend would be expected to select for later timing of migration and spawning. Thus, the advanced spawning date at all three hatcheries has occurred despite water temperature changes, not as a consequence of them. Warm temperatures likely provide a natural check against early spawning at the UW Hatchery because temperatures in early October (>15°C) approach lethal levels for chinook salmon and coho salmon embryos (Murray and McPhail 1988). However, the influence of ambient temperature has been weakened to some extent by the use of chilled water to improve survival rates of embryos from the earliest spawning chinook salmon at UW Hatchery.

The warming thermal regime in Lake Washington has not overcome the apparent selection in the hatchery for earlier spawning timing, but it was still evident in the correlation between the residuals of spawning and temperature (adjusted for the long-term trends). The correlation was significant for chinook salmon and strongest for the months of September and October, when chinook salmon would likely be migrating and entering the hatchery. The chinook salmon spawn soon after they enter the hatchery, which means that thermal effects on migration would also be correlated with spawning date. Because coho salmon, on the other hand, remain in the hatchery for about a month prior to spawning, factors affecting migration (e.g., temperature) might be less strongly correlated with spawning. In addition, coho salmon spawn later in fall than chinook salmon, when temperatures are cooler and the effects of lake warming might be less critical.

Acknowledgments

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