
**Genetic Variation of Return Date in a Population of Pink Salmon:
A Consequence of Fluctuating Environment and Dispersive Selection?**

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Genetic Variation of Return Date in a Population of Pink Salmon: A Consequence of Fluctuating Environment and Dispersive Selection?

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ABSTRACT: A genetic basis for variation in the date that anadromous salmon return to their natal or home stream was demonstrated by significant differences between return dates of pink salmon *Oncorhynchus gorbuscha* families. Of 120 families made by hierarchical matings of 60 males and 120 females, 118 families survived. The first half (60 families) and second half (60 families) were spawned 28 d apart. The 120 full-sibling families were incubated separately, released as fry with identifying coded microwire tags, and recovered entering the home stream as adults. Families in the first half returned on average 29 d before families in the second half ($P < 0.0001$). Average return dates differed between families that were spawned on the same day by different fathers ($P < 0.045$ sons; $P < 0.040$ daughters). These differences indicate that additive genetic variance contributes to the natural variation of return date. Heritability of timing of anadromous migration in odd-year pink salmon spawned in Auke Creek, Alaska, was very high, perhaps near unity, over the entire population. For segments of the population spawning on the same date, heritability was about 0.2 (SE 0.2) in males and about 0.4 in females (SE 0.2). We suggest that such high genetic variability of a trait closely related to fitness is maintained by the fluctuating environment to which Auke Creek pink salmon must continually adapt or by dispersive selection caused by redd superimposition. In either case, generalizing to other salmon populations, rational management must preserve variability of return timing if the fitness of populations is to be conserved.

INTRODUCTION

Timing of anadromous migration into their spawning streams is important to fitness of salmon metapopulations and their constituent demes. This dependence occurs because streamflow and temperature vary seasonally and interannually and because freshwater entrance and spawning can succeed only within limits of flow and temperature. The dependence of population fitness on the timing of the summer/autumn spawning immigration also occurs because for many populations, spawning occurs soon after entry into fresh water and the spawning date conditions the timing of fry emergence. This dependence is evident in the contrast between populations spawning in warmer and cooler rivers, in which development is slower and spawning migration occurs earlier in the year in populations inhabiting cooler streams (Sheridan 1962; Brannon 1987).

Hatchery and fishery management practices are potentially selective forces on return timing. If return timing variations have a significant genetic component, then reliance on early-returning or late-returning fish for hatchery broodstock would tend, over generations, to change the return timing of the broodstock. Evidence of such genetic variation of return timing in salmonid populations, in particular effective artificial selection on spawning season or return date, has been demonstrated in a captive broodstock of rainbow trout *Oncorhynchus mykiss* (Siitonen and Gall 1989; Su et al. 1997) and hatchery-bred steelhead *O. mykiss* (Millenbach 1973). There is also circumstantial evidence that artificially selective hatchery practices have been selective and responsible for changes of return timing; e.g., Cramer et al. (1991, p31) states, “The tendency of hatcherymen to use the first arriving [lower Columbia coho salmon *O. kisutch*] for brood is the predominant factor responsible for [the perennial occurrence of early-returning coho salmon in the run].”

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Fishing mortality related to fishery management practices may have had similar effects on the return timing of salmon populations (reviewed by Reisenbichler 1997). In Southeast Alaska in the 1920s a mixed stock fishery that harvested later rather than earlier returning pink salmon *O. gorbuscha* demes caused, over several generations, the average aggregate return timing to change to an earlier date and reduced the productivity of the regional metapopulation (Alexandersdottir 1987.) Similarly, differential harvest rates of the coho salmon population in the lower Columbia River caused later migrations in some demes. (Cramer et al 1991.)

A change of return timing would be expected to reduce a deme's average fitness in its natural wild environment, where natural selection is important. Fish returning to the stream too early may encounter temperatures too high and flow too low to permit spawning, and fish returning too late may encounter flows too high. In a hatchery broodstock a change of return timing may not affect fitness because hatchery broodstocks do not necessarily depend on encountering optimum conditions. However, if the hatchery-changed broodstock were to interact genetically with wild demes — i.e., if significant numbers of hatchery-bred fish were to breed with wild demes — then the fitness of those demes might be reduced (reviewed by Reisenbichler 1997).

Such predictions of changeable return timing follow from the assumption that variation of return timing in salmon metapopulations and demes has a significant basis in genetic variation — that is, that heritability of return timing is significant in salmon populations. Return timing is commonly held to be a genetically based characteristic of salmonid populations (e.g., Ricker 1972), but no genetic analysis of return timing has been made in any population. Genetic analyses of the related trait spawn date have been made for cultured rainbow trout (Siitonen and Gall 1989; Su et al 1997), but this was an artificially bred population not living in a wild environment. Indeed most estimates of heritability of life history traits in salmonids have been made in artificially bred populations that grew to maturity in artificial environments, including the 10 estimates of heritability of salmonid life history traits included in Mousseau and Roff's (1987) review of wild, outbred animal populations. Because natural and artificial environmental variation can differ and because genetic variation may also differ in artificially bred and wild populations, estimates of heritability of life history traits made in cultured broodstocks and under artificial environments may not be indicative of the actual heritabilities in wild, out-

bred populations. Knowledge of any genetic basis for return timing is needed as a basis for salmon conservation policy.

Understanding this need, we estimated the genetic component influencing variation of spawning run timing in a population of pink salmon in Auke Creek, in Juneau, Alaska. We analyzed variation of return date within and between families created by breeding parents randomly sampled from a wild population and releasing the families of progeny to the natural environment.

Auke Creek Pink Salmon

Auke Creek is the short (350 m) and steep (falling 20 m) outlet stream of Auke Lake. Stream and intragravel temperatures in July average 15.5°C and can range above 18°C (potentially sterilizing to pink salmon gametes; W. W. Smoker, unpublished data), average 14.4°C in August, 11.4°C in September, and 1.5°C in winter. (Fukushima and Smoker 1997). Streamflow, which varies with rainfall and snowmelt, is least in summer and can be nearly nil for extended periods in July and August, precluding pink salmon entrance. Streamflow is greatest in autumn, sometimes scouring the streambed and also precluding entrance of adult salmon (July mean 0.36 m³·s⁻¹, September mean 0.81 m³·s⁻¹, September peak daily discharge >15 m³·s⁻¹). Lake Creek, the inlet to Auke Lake has a lesser but more variable streamflow and is cooler in summer (summer monthly averages all <11°C). (Data are on file at U.S. National Marine Fisheries Service, Auke Bay Laboratory, Juneau, Alaska, and are here summarized from Fukushima and Smoker 1997).

Auke Bay, which receives Auke Creek, is the marine nursery environment where Auke Creek pink salmon fry first feed. Its climate varies strongly over the seasons. It is cold (near 0°C) and vertically mixed in winter. In spring the surface warms above 4°C, usually in early April, only then permitting substantial growth of salmon. Auke Bay stratifies in late April or early May, and the surface temperature rises above 10°C after May. Phytoplankton and zooplankton bloom in April and May each year; the spring bloom varies in intensity from year to year (Coyle et al. 1990; Ziemann et al. 1991).

In each of the odd- and even-year populations of pink salmon there are 2 temporal groups of adults that enter Auke Creek, separated by a hiatus near 1 September. About 20 d separates their median arrival dates in both odd and even years (Taylor 1980; Gharrett and Smoker 1993b). Annual censuses since 1971 (counts of individual salmon at Auke Creek Weir, situated at

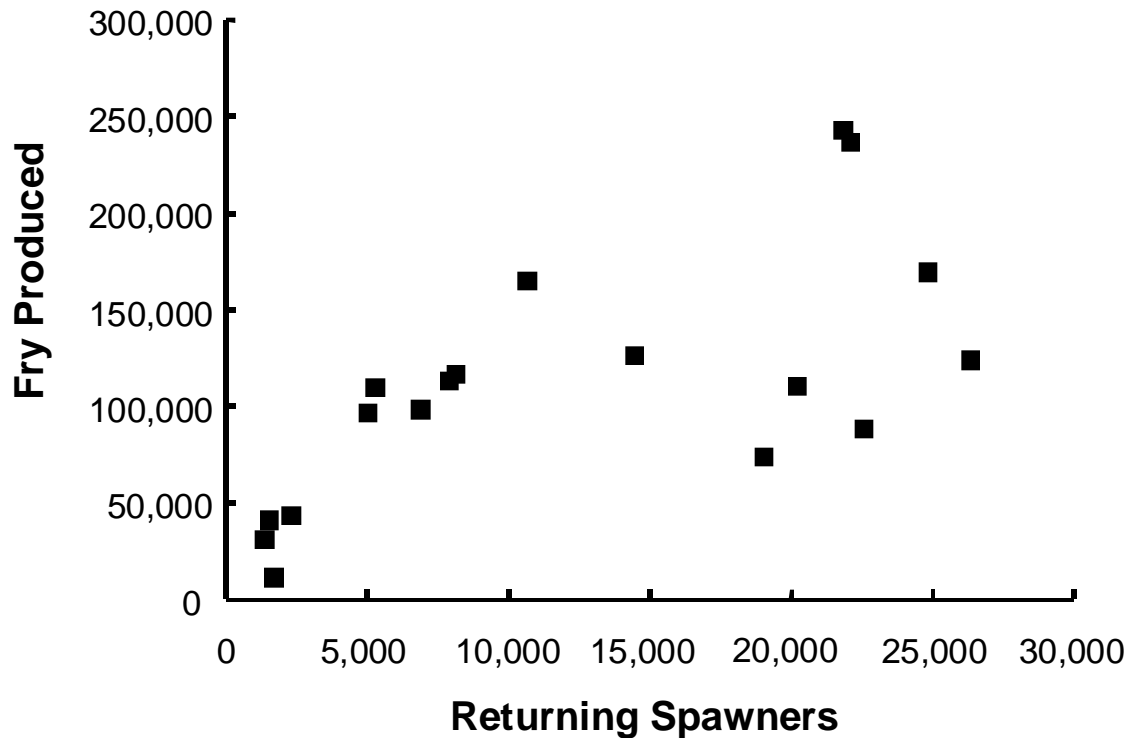


Figure 1. Numbers of adult pink salmon entering Auke Creek and numbers of fry leaving Auke Creek the following spring, brood years 1979 to 1996. Data from Taylor and Lum 1998.

the mouth above high tide) have recorded 1,548–26,317 adults entering Auke Creek between late July and late September (Taylor and Lum 1998).

They spawn within 5–10 d, either in Auke Creek or in Lake Creek, the major inlet stream for Auke Lake (Fukushima and Smoker 1997). Fukushima and Smoker (1997) observed more than 1,000 pink salmon spawners in Lake Creek in 1992, 1993, and 1994. They observed that 30–70% of daily cohorts of tagged adult immigrants migrated to Lake Creek in 1994 when the total census was 22,548, second highest in history. However, few Lake Creek spawners were observed between 1978 and 1982, years when the total censuses were also high, exceeding 10 thousand each year. The use of Lake Creek spawning habitat may be a recent phenomenon in Auke Creek pink salmon.

The offspring leave as fry between mid March and late May. Censuses since 1980 (daily counts at Auke Creek Weir) have shown between 31,000 and 243,000 fry leaving Auke Creek each year (Taylor and Lum 1998). Since 1980 the number of fry produced has been directly proportional to the number of returning parent adults for brood years in which the number of adults was less than about 10,000, but not directly proportional otherwise (Figure 1). Unlike the adult immigration, the timing of fry emigration is not obviously

bimodal, but genetic experimentation has demonstrated that offspring of late-returning adults emigrate on average 20 d later than offspring of early-returning adults (Gharrett and Smoker 1993a). Studies of tagged Auke Creek pink salmon fry during April and May have shown that growth in nearshore Auke Bay is faster at warmer temperatures, that water temperature increases during the spring, and that survival to adulthood is correlated with fry growth rate during this period (Mortensen et al 1991). Pink salmon fry leave the nearshore habitat of Auke Bay at the end of May and are gone from Auke Bay entirely by mid July (Mortensen et al 1991).

Several lines of evidence suggest that life history variation between early- and late-returning Auke Creek pink salmon is adaptive and important to overall population fitness. One is that the difference of migration timing of early- and late-returning adults in Auke Creek is associated with subtle but detectable, biochemical genetic variation (McGregor et al 1998), suggesting that the difference may be an evolved difference based on genetic variation. A second line of evidence is that offspring of early-returning pink salmon in Auke Creek tend to complete embryonic development more slowly at a given temperature than do offspring of late-returning salmon (Joyce 1986; Goddard 1995; Hebert et al.

1998). The result is the synchronization of emergence of offspring in the subsequent spring with the spring bloom, despite considerably warmer incubation for the offspring of early-returning salmon. Third, in at least one recent year, relatively more early-returning pink salmon spawned in Lake Creek and relatively more late-returning fish spawned in the outlet, Auke Creek (Fukushima and Smoker 1997). Lake Creek is cooler, which means that incubation time for offspring of early-returning salmon tends to be longer, so this difference in habitat also tended to synchronize emergence of offspring with the spring bloom.

Auke Creek pink salmon are similar to many other pink salmon populations in their season of immigration and spawning, in their bimodal pattern of immigration, in their use of different spawning habitats within a drainage, in their season of fry emigration, and other aspects of their life histories (reviewed by Heard 1991).

METHODS

Breeding Experiment

We crossed 60 males with 120 females so that each male was crossed to 2 of the females (Smoker et al. 1994). This produced 120 families composed of full siblings. Because half or 60 of the 120 families had a male parent in common, there were 60 families of half siblings (combined progeny of 2 crosses with the same male). The parents were selected from the 1983 run in Auke Creek by a random sample stratified by time. Half were sampled and spawned together near the peak of migration on 17 August; the other half were spawned near the later peak on 20 September. We incubated each full-sibling family in 3 replicate incubator compartments and randomly assigned them to positions in an array of incubators.

At completion of development we tagged, with coded microwires, all or a sample of fry from 120 full-sibling families, using one code per family (Thrower and Smoker 1984). Our design called for releases of 1,000 fry per full-sibling family, but a few families were reduced to a few fish at tagging. The number tagged ranged from 56 to 1,138. Each fish was also marked by excision of its adipose fin. The average weight of these unfed fry was 0.25 g. We released the August-spawned families on 28 March and the September-spawned families on 3 April 1984, coinciding with wild fry emigration from Auke Creek.

In 1985 all 26,317 pink salmon entering Auke Creek were examined. There were 1,890 with missing

adipose fins. Of those marked adult pink salmon, 1,307 retained tags representing 59 half-sibling and 118 full-sibling families. Date of entry into Auke Creek and other data for each fish were recorded. Technicians of the Alaska Department of Fish and Game Coded Wire Tag Laboratory recovered and decoded the tags. Their procedure required agreement between 2 independent decoders.

Analysis

We analysed the hierarchical linear model,

$$\text{Date of Return} = \mu + C_i + S_{j(i)} + D_{k(j,i)} + e_{ijkl} ;$$

μ = the population mean date of return,

C_i = the fixed effect of the i th date of spawning on date of return,

$S_{j(i)}$ = the random effect of the j th father within the i th date of spawning,

$D_{k(j,i)}$ = the random effect of the k th mother mated to the j th father, and

e_{ijkl} = random error.

We used the General Linear Models (GLM) procedure in the SAS statistical analysis programs (SAS 1985) to evaluate this model and ran the analysis under the VAX VMS operating system. We tested significance of date, father, and mother effects by approximate F -tests (Searle 1971, Chapter 6) and estimated components of variance and heritabilities, and standard errors of the estimates, from the intraclass correlations that followed formulas given in Becker (1984). We estimated heritability as $4 \times$ the ratio of the father component of variation to the sum of the father, mother, and error components.

RESULTS

The 1,307 returning tagged pink salmon represented 118 full-sibling and 59 half-sibling families. Those spawned 20 August 1983 returned between 25 July and 16 September 1985. The average dates of return for the individual families spawned on 20 August 1983 ranged from 4 August to 23 August 1985 and the overall mean of the family averages was 14 August 1985 (Figure 2). Fish spawned 17 September returned between 4 August and 23 September 1985; the average dates of return of the families ranged between 3 September and 17 September, and their overall mean was 12 September 1985 (Figure 2).

Because sons returned on average 3–4 d earlier than daughters, we analyzed dates of return of sons

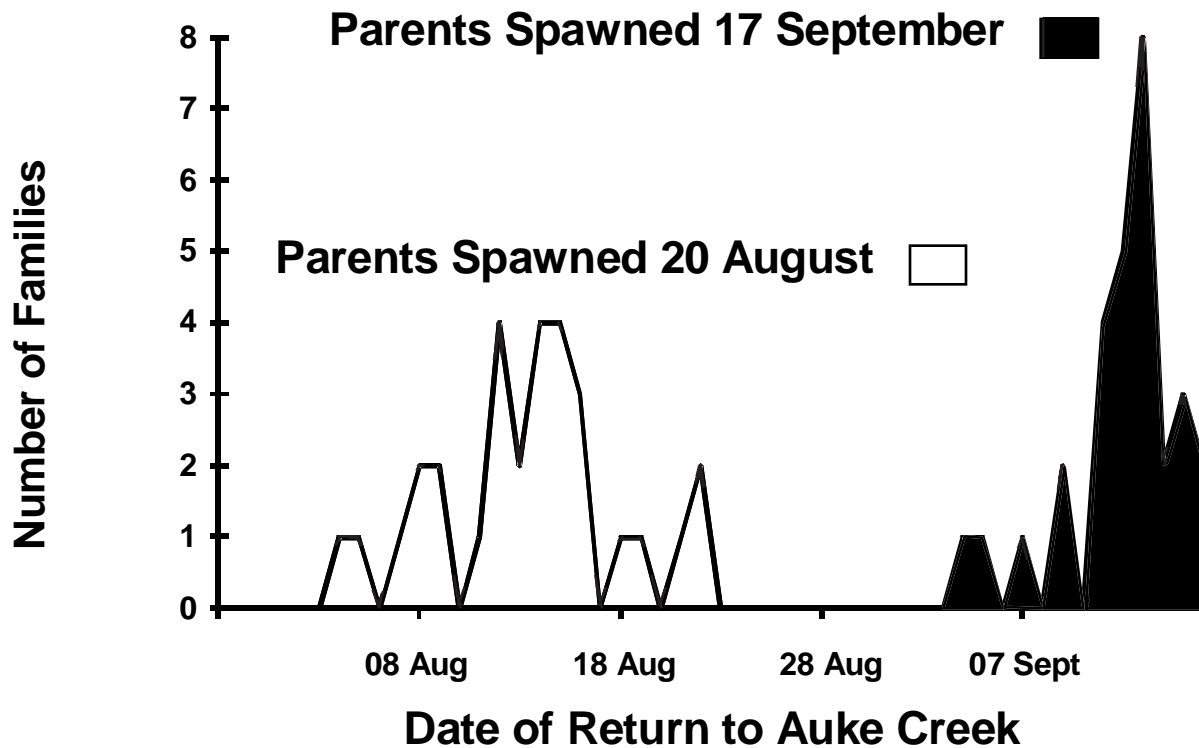


Figure 2. Frequency of average dates of return to Auke Creek of 59 half sib families of pink salmon in 1985; 29 families resulted from 20 August 1983 spawnings of 30 males each with 2 different females and 30 resulted from 17 September 1983 spawnings. Date of spawning significantly affected return date of either males or females ($P < 0.0001$), differences that may be genetically mediated. Average return date of females ($P < 0.0400$) and males ($P < 0.0447$) varied significantly among sires implying detectable additive genetic variation of return date within segments of the population spawning on the same day.

separately from dates of return of daughters. The number of sons ranged from 0 to 31 and the number of daughters from 0 to 20 per half sibling family. Of the 120 full-sibling families, 118 were represented by at least one family member.

The date of spawning, which is closely related to the parents' return timing, had a significant effect on return date of F_1 sons ($F_{1,57} = 818.94$, $P < 0.0001$) and F_1 daughters ($F_{1,57} = 732.51$, $P < 0.0001$). Average dates of return for families spawned 20 August did not overlap with the average return dates for families spawned on 17 September (Figure 2).

Fathers of same-day breedings produced offspring with significantly different return timing, evidence of an additive genetic contribution to variation of return date. Different fathers within each breeding date had a significant effect on return date of daughters ($F_{57,48} = 1.73$, $P < 0.0234$), but may or may not have had a significant effect on return date of sons ($F_{57,48} = 1.37$, $P < 0.1336$). Similarly, the effect of mothers bred with fathers within each breeding date was significant on the return dates of both sons ($F_{48,611} = 1.42$, $P < 0.0362$) and daughters ($F_{52,476} = 1.38$, $P < 0.0447$).

By analyzing mean dates of return of families, rather than of individual dates of return, we also examined the significance of effects of fathers on sons and on daughters. That analysis has the advantage of not being influenced by family size but did not permit a test of mother effects or an estimate of heritability. It demonstrated a significant effect of fathers on return dates of sons ($F_{57,48} = 1.62$, $P < 0.0447$) and a significant effect of fathers on return dates of daughters ($F_{57,52} = 1.62$; $P < 0.0400$).

Heritability of return date, estimated from the effect of fathers bred on the same date, was 0.39 (SE = 0.19) among daughters and 0.18 (SE = 0.16) among sons.

DISCUSSION

Genetic variability is detectable as a component of the variability of the timing of anadromous migration, both in segments of the population spawning on particular days during the season and, with some ambiguity, in the entire population of Auke Creek pink salmon. The

largest factor contributing to timing variation among the families we observed was the date of breeding — i.e., variation between August- and September-spawned families. We cannot partition that variation into genetic and environmental components because the 2 groups of families were incubated in 2 different temperature regimes. One regime began in August when temperature in Auke Creek is near 15°C, and the other began in September when Auke Creek had cooled to about 10°C. The 2 groups of families were also released on different days. However, it seems unlikely that return timing variation would be related to environmental variation during embryogeny and early life, so it seems likely that a major part of the observed difference in return timing is genetically based. The interval between early- and late-returning families in 1985 was 1 d longer than the interval between their spawnings in 1983; if we assume that environmental differences between the groups had no effect on return date, this observation suggests that nearly all of the variability of return date is genetic in the entire population of early- and late-returning Auke Creek pink salmon. That is, heritability of return date in the entire population may be near unity.

Our demonstration of between-family and within-spawning-day variation of return timing is unambiguous evidence of genetic variation. It suggests that 40% of the variation of return date in a segment of the population (i.e., among offspring spawned on the same day) is due to additive genetic variation, a moderately high heritability.

Return timing is closely allied to fitness of Auke Creek pink salmon because the suitability of the habitat for the spawning immigration and for spawning itself changes during summer and autumn. In midsummer streamflow is likely to be too low and temperature too high to permit successful immigration and spawning. During autumn increasingly frequent freshets prevent successful immigration and spawning. Return timing is also closely allied to fitness because it determines the limits of timing of spawning, which in turn determine the timing limits of fry emergence. Emergence timing must be synchronized with the seasonally changing suitability of Auke Bay if fry are to attain rapid growth and high survival.

Our estimates of heritability of return timing within segments of the population are imprecise, and the true heritability may not be much greater than zero. Even in that case, however, our analysis of individual dates of return provides strong evidence of a genetic contribution to variability of return timing in population segments. That evidence is corroborated by our analysis

of a more balanced set of data: family mean dates of return.

Although significant genetic variability of life history traits has been observed in this and other salmonid populations (e.g., Smoker et al. 1994, Su et al. 1997, Geiger et al. 1998, Smoker et al. *in review*), heritabilities of life history traits, even as high as 0.4, are unusual in wild, outbred populations of ectothermic vertebrates (Mousseau and Roff 1987). Evolutionary genetic theory predicts that heritabilities of life history traits would be small (reviewed by Mousseau and Roff 1987). Fluctuations of a selective environment, either temporal (e.g., between years) or spatial (e.g., between microhabitats), are one mechanism by which genetic variation of a life history trait, and therefore high heritability, could be maintained in a population. (Ewing 1979; Gharrett and Smoker 1993b; Geiger et al. 1998). Another potential mechanism we propose is dispersive selection acting on return date.

Fluctuating Environment

The environment of Auke Creek pink salmon, as characterized by the seasonal patterns of changing streamflow and temperature, fluctuates both temporally from year to year and spatially from site to site (Fukushima and Smoker 1997). The changing seasonal pattern in their nursery area also fluctuates from year to year (Coyle et al. 1990; Ziemann 1991). Genetic variation and high heritability of a life history trait, like return timing, are probably maintained by the fluctuating environment of Auke Creek pink salmon. In some years the fitness of early-returning salmon is favored by (1) cool stream water and moderate streamflow, which allow them to spawn successfully in midsummer; (2) cool intragravel water in late summer, which induces slow embryonic development and later emergence of their offspring in synchrony with the spring bloom; or (3) by early warmth in the surface waters of Auke Bay, which engenders rapid growth and high survival of their early-emerging offspring. In other years, late-returning salmon are favored.

Spatial fluctuations are evident in the different streamflows and temperatures of Auke Creek and Lake Creek (Fukushima and Smoker 1997). The fitness of early-returning salmon may be favored by use of Lake Creek as spawning habitat, rather than Auke Creek. Because Lake Creek is cooler, offspring develop more slowly and emerge later and will therefore be more likely to emerge in synchrony with the spring bloom. Conversely, fitness of early-returning salmon spawning in Lake Creek may be reduced by midwinter dessication and freezing compared to Auke Creek. Both

temporal and spatial fluctuations could act selectively to maintain both alleles determining early return and alleles determining late return in the Auke Creek population of pink salmon.

Dispersive Selection

Dispersive selection, dependent on the abundance or density of spawners in a generation, could also contribute to the maintenance of genetic variation of run timing. Redd superimposition is the major source of density dependent mortality of pink salmon embryos (McNeil 1964). Late-returning adults may, through redd superimposition, disturb embryonic offspring of early-returning salmon. The younger of those disturbed embryos may be killed because embryos are resistant to mechanical disturbance only after completion of epiboly, about 2 weeks after spawning in the warm water encountered by early-run salmon (Hebert et al. 1998.) A disturbance might therefore be less likely to destroy more advanced embryonic offspring older than 2 weeks. The result would be relatively high survival of the earliest and latest spawners' offspring and relatively low offspring survival for spawners returning around the middle of the run.

This hypothetical selection-based mechanism would tend to maintain genetic variation of return date in the population and would explain the bimodal structure of return timing observed in both odd- and even-year Auke Creek pink salmon, even if redd superimposition and differential selection did not occur in every generation. Redd superimposition becomes likely only as the cumulative density of spawners increases (McNeil 1964), so alleles determining early return would be maintained because offspring of salmon possessing them would complete epiboly and be resistant to disturbance by later spawners. Some copies of alleles determining mid-run return would be lost because offspring of salmon possessing them would not complete epiboly before disturbance by later spawners and would be likely to die if disturbed; alleles determining late return would not be affected by disturbance.

Several observations of Auke Creek pink salmon tend to support a dispersive selection hypothesis:

- (1) High spawner density occurs frequently. In 12 years from 1971 to 1997 the weir census exceeded 10,000 (Taylor and Lum 1998). Above that census number, the number of fry produced historically has not been directly proportional to the number of spawners (Figure 1; Fukushima 1996, chapter 3).
- (2) Significant numbers of embryos were directly observed (1994) to be disturbed and dislodged from gravel in direct relationship to daily variation of spawner abundance (Fukushima et al 1998). Before 10 September, dislodged eggs were mostly dead, whereas after 19 September dislodged eggs included many live embryos at advanced, resistant stages of development.
- (3) In studies of 3 different brood years including both odd and even lines, embryos from early-returning Auke Creek pink salmon tended to progress through the vulnerable stages of epiboly more quickly than did embryos from late-returning salmon, even in the laboratory at the same temperature. This suggests that pre-epiboly development in early-run pink salmon has responded to some selection not experienced by late-run salmon (Joyce 1986; Goddard 1995; Hebert et al 1998). Development time from spawning to hatching, however, was longer at a given temperature for the offspring of early-returning salmon in each study, confirming the relationship observed in other salmon (e.g., Brannon 1987).
- (4) Offspring of early-run pink salmon in at least 3 years have suffered higher intragravel mortality than those of late-run salmon (A. J. Gharrett, unpublished analysis of genetic tag data).
- (5) Fecundity of early-run pink salmon is greater than that of late-run pink salmon, and heritability of fecundity is high (author's unpublished data); higher fecundity might have evolved in association with early return as a consequence of greater mortality in early-spawned embryos.

An argument against the dispersive-selection hypothesis is that some advanced (therefore resistant) embryos from the earliest spawners when disturbed by redd superimposition by late spawners would be required to survive after being disturbed, or else alleles determining earliest return would not be preferentially maintained. Disturbed embryos that are actually dislodged from the gravel into the stream, even if they survive the shock of disturbance, are unlikely to survive either transport downstream into the bay or predation by fish (Reed 1967), gulls (Moyle 1966), or other predators. However, probably not all embryos disturbed by redd superimposition are dislodged from the gravel but may remain buried and may survive if they are resistant to mechanical shock. Observations of live postepiboly embryos in a redd immediately af-

ter superimposition would lend strong support to the dispersive selection hypothesis, but are lacking.

McNeil (1964) recognized that redd superimposition is an important source of mortality in pink salmon embryos and that fitness of late-spawning fish might therefore be favored, even though embryos deposited in the middle portion of the run otherwise have the highest survival potential. He hypothesized that hereditary differences associated with time of spawning do not exist within stocks and that mortality from redd superimposition does not therefore act as a selective force on timing of return and spawning. It is now clear that such hereditary differences are important, and it is important to explain how alleles determining early return can persist in the face of redd superimposition. The dispersive-selection hypothesis, in which some postembryonic embryos from the earliest spawners survive redd superimposition, is a plausible explanation.

Adaptive Variation and Heterogeneity of Gene Frequencies

Variability of run timing and of other fitness related traits is apparently important to the adaptability and fitness of Auke Creek pink salmon and of other salmon populations. In the face of climatic variability, the adaptive strategy of pink salmon apparently includes

population variability of return timing, a strategy that tends to ensure that some adults encounter suitable conditions each generation. This adaptively important genetic variation of run timing can be readily observed, despite the subtlety of the timing-based heterogeneity of allozyme gene frequencies in Auke Creek pink salmon (McGregor et al. 1998). Such surveys of genetic structure of salmon populations by biochemical genetic techniques may not reveal the importance of genetic variation expressed as adaptively important phenotypic variation. One reason for this is that much of allozyme variation may be neutral or nearly neutral, and a small amount of gene flow homogenizes allele frequencies among temporally separate subpopulations. Variation in life history-related traits of Auke Creek pink salmon, like timing of migration or body size and fecundity (Smoker et al. 1994; author's unpublished data), would probably be much more sensitive to natural selection than would neutral alleles coding for allozymes. Maintenance of variability of these life history traits in wild populations and metapopulations is probably crucial to the long-term fitness of the populations (Gharrett and Smoker 1993a, 1993b; Geiger et al. 1997). Rational hatchery management and fishery management should take into account variability of life history traits and act to conserve it, particularly in wild populations.

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