Determinants of stream life, spawning efficiency, and spawning habitat in pink salmon in the Auke Lake system, Alaska

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Abstract: Variation in stream life, spawning efficiency, and spawning habitat among adult pink salmon (*Oncorhynchus gorbuscha*) in the Auke Lake system, southeastern Alaska, was best explained by stream discharge, stream temperature, and a combination of stream temperature and discharge. We estimated these attributes of female pink salmon spawners in samples of daily cohorts tagged as they entered fresh water and used generalized linear models to analyze variation in the attributes with respect to environmental factors. Spawners varied in stream life (5–11 days), spawning efficiency (30–70% of females in daily entry cohorts retained less than 500 eggs at death), and spawning habitat (30–70% spawned in the lake outlet stream rather than the lake inlet stream). Observed variation of habitat (proportionately more use of the cooler inlet stream early in the spawning season when stream temperatures are warm and development is rapid) would contribute to synchronicity of fry emigration, which is known to be positively correlated with subsequent survival in Auke Lake pink salmon.

Résumé : La variation du séjour en cours d'eau, de l'efficacité du frai et de la zone de frai chez les saumons roses adultes (*Oncorhynchus gorbuscha*) du bassin du lac Auke, dans le sud-est de l'Alaska, s'expliquait le mieux par le débit du cours d'eau, la température du cours d'eau et une combinaison de la température et du débit du cours d'eau. Nous avons estimé ces caractéristiques chez des reproducteurs femelles de saumon rose dans des échantillons de cohortes quotidiennes marquées à leur entrée en eau douce et nous avons utilisé des modèles linéaires généralisés pour analyser la variation dans les caractéristiques par rapport aux facteurs environnementaux. Les reproducteurs ont montré une variation en ce qui a trait au séjour en cours d'eau (5–11 jours), à l'efficacité du frai (30–70% des femelles dans les cohortes quotidiennes d'arrivée en eau douce portaient moins de 500 oeufs à leur mort) et à la zone de frai (30–70% dans l'émissaire du lac plutôt que dans son affluent). La variation observée de l'habitat (utilisation proportionnellement plus grande de l'affluent plus froid tôt au cours de la saison de frai lorsque les températures du ruisseau sont plus froides et le développement est rapide) contribuerait à la synchronisation de l'émigration des alevins, que l'on sait corrélée positivement à la survie subséquente du saumon rose du lac Auke.

[Traduit par la Rédaction]

Introduction

In Pacific salmon (*Oncorhynchus* spp.), variation in spawning timing between streams within limited geographical areas is such that early runs occur in streams with temperatures cooler than those receiving late-run spawners (Sheridan 1962; Saunders 1967; Burger et al. 1985; Brannon 1987). Furthermore, adaptive variation in embryonic development rate, whereby embryos incubating in colder water require fewer accumulated temperature units to complete development, has been observed between species and between populations of the same species (Koski 1975; Joyce 1986; Brannon 1987; Hebert 1994). The important outcome of such migratory traits and embryonic development patterns is the relatively synchronous emigration of fry and smolts from different run timings into the first feeding area, i.e., an estuary or a lake (Randall et al. 1987). Synchrony of fry and smolt emigration in Pacific salmon in the spring maximizes survival to maturity if the emigration peak coincides with seasonal optimal conditions for their growth or overwhelms predators; such a match between emigration timing and optimal conditions has been demonstrated for several populations (Brannon 1987).

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We studied variation in three attributes of pink salmon spawners in the Auke Lake system in southeastern Alaska that may influence timing of fry emigration, i.e., (*i*) stream life, (*ii*) spawning efficiency, and (*iii*) habitat. We simultaneously studied the relationship among these attributes and environmental factors measured during the spawning season. Our hypothesis is that each attribute should vary within the season in such a way that synchrony of fry emigration would be maximized. In other words, for the fry to achieve synchronous emigration, (*i*) the stream life of spawners needs to decrease as the spawning season progresses so that eggs from whole cohorts are spawned in a relatively short period, (*ii*) the spawning efficiency needs to be relatively higher during the middle part of the season than the early and late parts of the season so that pink salmon fry are mostly represented by cohorts that entered the system with a similar timing, or (*iii*) spawners need to select a warmer stream in the system for egg deposition later in the season than they do earlier in the season so that development is accelerated in embryos from the later spawners relative to development in embryos from the earlier spawners.

Fig. 1. Map of the study area, showing Auke Creek, Lake Creek, and Auke Lake.

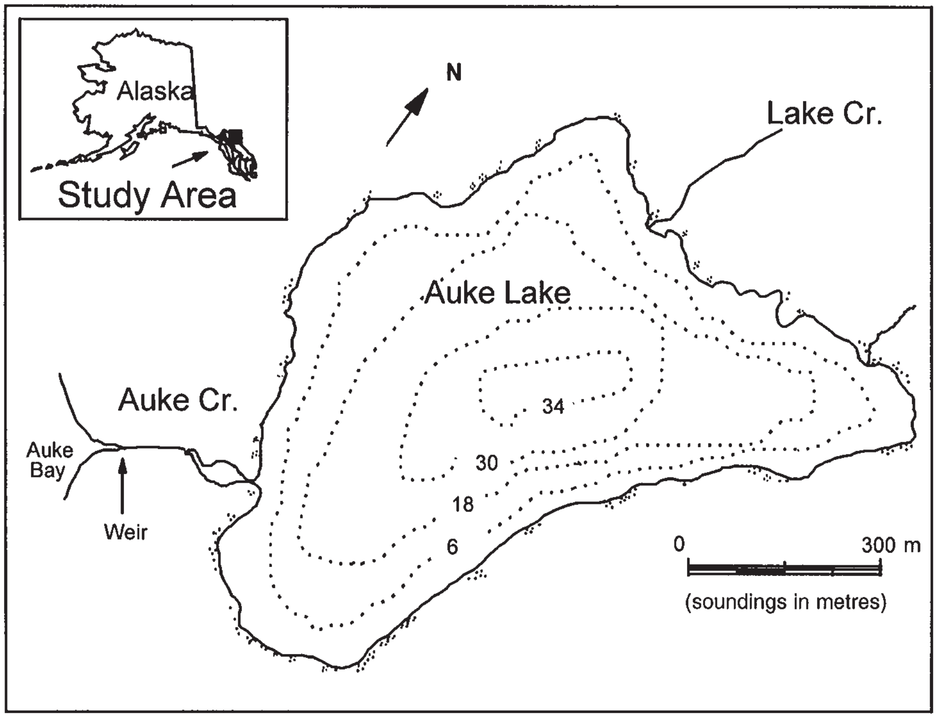


Table 1. Monthly means of stream temperature and discharge of Auke and Lake creeks from July to December during 1965–1972.

	Auke Creek	Lake Creek
Stream temperature (°C)		
July	15.5±2.4	10.8±1.8
August	14.4±1.9	10.4±1.7
September	11.4±1.6	7.8±1.7
October	7.4±1.7	4.8±1.8
November	4.0±1.5	1.5±1.4
December	1.5±0.7	0.5±0.5
Stream discharge ($m^3 \cdot s^{-1}$)		
July	0.36±0.43	0.32±0.62
August	0.65±0.62	0.62±1.13
September	0.81±0.71	0.67±0.81
October	0.67±0.53	0.46±0.62
November	0.44±0.48	0.29±0.59
December	0.19±0.18	0.09±0.14

Note: Values are given as means ± standard deviation. Dates are from the records of U.S. Geological Survey, on file at U.S. NMFS Auke Bay Laboratory, Juneau, Alaska.

Methods

Study site

The Auke Lake system supports populations of sockeye salmon (*Oncorhynchus nerka*), coho salmon (*Oncorhynchus kisutch*), chum salmon (*Oncorhynchus keta*), and pink salmon (*Oncorhynchus gorbuscha*). Pink salmon escapement into the system has varied from 1700 to 26 000 in recent years (1977–1994; data on file, U.S. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Auke Bay Fisheries Laboratory, 11305 Glacier Highway, Juneau, AK 99801, U.S.A.). In the Auke Lake system, pink salmon spawn in two major spawning habitats, Auke and Lake creeks. Auke Creek is a short and steep lake-fed outlet stream that flows approximately 350 m from Auke Lake; Lake Creek is the major tributary inlet (Fig. 1). The spawning migration occurs during August and September, usually with two distinct modes referred to as early and late runs; the peak immigration of the early-run spawners normally precedes that of the late-run spawners by more than 2 weeks (Taylor 1980; Gharrett and Smoker 1993).

Auke Creek and Lake Creek offer different spawning and incubation habitats to pink salmon in terms of stream temperatures and discharge (Table 1). Maximal stream temperatures normally occur during July, when average temperatures in Auke and Lake creeks exceed 15 and 10°C, respectively. Lake Creek temperatures are uniformly lower than those of Auke Creek, and the difference is greatest during summer. During winter, Lake Creek temperatures drop to near 0°C, while Auke Creek temperatures remain above 1°C. Pink salmon eggs deposited in Auke Creek may be subject to lethal high temperature during summer, whereas eggs deposited in Lake Creek may be subject to lethal low temperature during winter (Combs 1965).

Stream discharge reaches its peak in September in both creeks. On average, Lake Creek discharge is always smaller than that of Auke Creek as a natural consequence of geomorphology. However, Lake Creek discharge, being unregulated by the buffer effect of Auke Lake, shows greater variation owing to freshets and droughts than does Auke Creek. Also, the eggs developing in Lake Creek may be subject to mechanical shock and washout, which can be a significant mortality source especially before the eyed stage (Smirnov 1954).

Despite the time lag between the runs and despite a decline from the early immigration peak to the late of more than 5°C in stream temperature, the emigration of pink salmon fry the next spring is relatively synchronous; the time span of fry emigration (2.5–97.5% emigration) is not amplified beyond the time span of adult immigration (2.5–97.5% immigration) as might be predicted from consideration of the steeply declining temperature of Auke Creek each autumn (Fig. 2).

Tagging

Tagging was conducted at the weir located immediately above the intertidal zone of Auke Creek from August 23 to September 21, 1994. Throughout the spawning season, spawners were counted manually and released upstream by the National Marine Fisheries Service (NMFS). Although a small number of pink salmon adults started to enter Auke Creek in late July, the period of tagging encompassed about 98% of the 1994 escapement (21 312 fish) of pink salmon. Numbered spaghetti tags were placed at the posterior insertion of the dorsal fin in female pink salmon randomly selected during the weir operation. The number of tagged fish was roughly proportional to the daily escapement of pink salmon (Appendix 1).

The tags were recovered each day and recorded from carcasses or as lost tags in Auke Creek, mostly at the weir, which eventually trapped all carcasses flushed downstream when stream discharges were sufficiently high. When the stream discharges were low, especially during the early spawning season, daily foot surveys were conducted throughout the entire channel of Auke Creek to collect tagged carcasses stranded on spawning grounds. Thus, almost all of the carcasses of pink salmon in Auke Creek were checked for the presence of tags. However, a small proportion of lost tags were not recovered when the stream discharges were extremely high.

Tag recovery was not conducted in Lake Creek, but the spawners in this creek were visually counted during foot surveys on the entire spawning ground (approximately 1300 m long) on 15 occasions throughout the spawning season to observe the temporal migration pattern of female pink salmon into Lake Creek.

Spawner attributes

Stream life L of female pink salmon was recorded in Auke Creek from 584 tagged carcasses throughout the spawning season as the time difference between tagging and recovery dates. The tagged carcasses were nearly all recently dead, but some were not. To construct as accurate a regression model as possible, lost tags and old carcasses were excluded from the calculation of stream life. Letting the number of carcasses tagged on the ith day and subsequently inspected for stream life be n_i, L_i was obtained as

$$L_i = \frac{1}{n_i}\sum_{j}^{n_i} L_{ij}$$

Note that, because no tag recovery was conducted in Lake Creek, stream life in this analysis applies only to Auke Creek spawners.

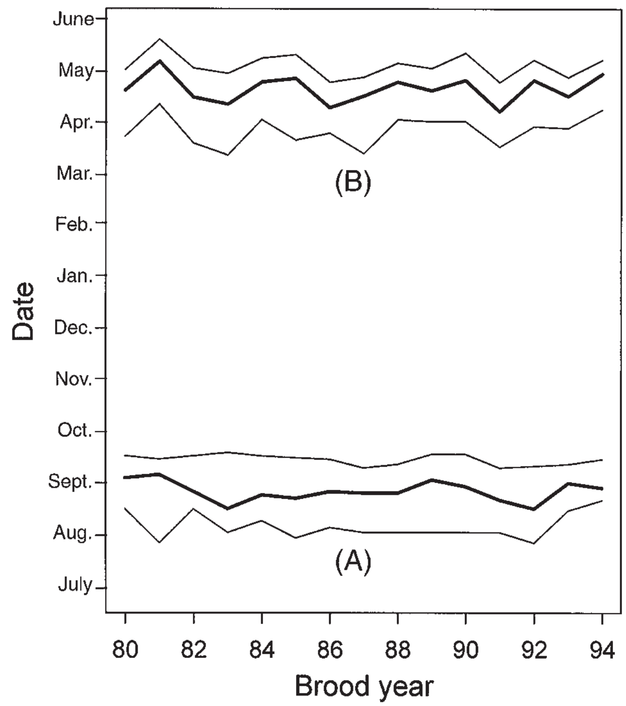
Spawning efficiency E of female spawners was evaluated in terms of the egg retention of carcasses. Four hundred and ninety-seven tagged carcasses were inspected for egg retention throughout the spawning season in Auke Creek. Instead of counting all the eggs retained in an ovary, egg retention was recorded simply as a binary response, i.e., many or few, corresponding to egg retention of more than or less than 500 eggs. Letting the number of carcasses tagged on the ith day and subsequently inspected for the egg retention be n_{ei}, of which s_i carcasses had less than 500 eggs, the spawning efficiency of the daily cohort of pink salmon on the ith day was obtained as $E_i = s_i / n_{ei}$, which again applies to Auke Creek spawners only.

Habitat, or the proportion P of females that spawned in Auke Creek, was obtained as $P_i = r_i / M_i$, where M_i is the number of fish tagged on the ith day and r_i is the number of tags from M_i subsequently recovered in Auke Creek. Lost tags were included in r_i, as those tags were most likely separated from the body of an Auke Creek spawner when the fish's tissue became softer as it decomposed. The three spawner attributes L, E, and P have 21 observations, as the tagging was conducted for a total of 21 days (Appendix 1).

Statistical analysis

Stream life L was analyzed by linear regression with different weights in the least square analysis, such that

Fig. 2. Timing of adult immigration into and fry emigration from the Auke Lake system for the 1980–1994 broods of pink salmon. Cumulative 2.5 and 97.5% timings (thin lines) are shown below and above 50% timing (thick lines) both for adults (A) and fry (B) (data from NMFS Auke Bay Laboratory, Juneau, Alaska).



$$w_i = 1/V(L_i) = (n_i - 1) \Big/ \sum_{j}^{n_i} (L_{ij} - L_i)^2$$

The L_i values were log-transformed to obtain a more linear relationship with predictor variables.

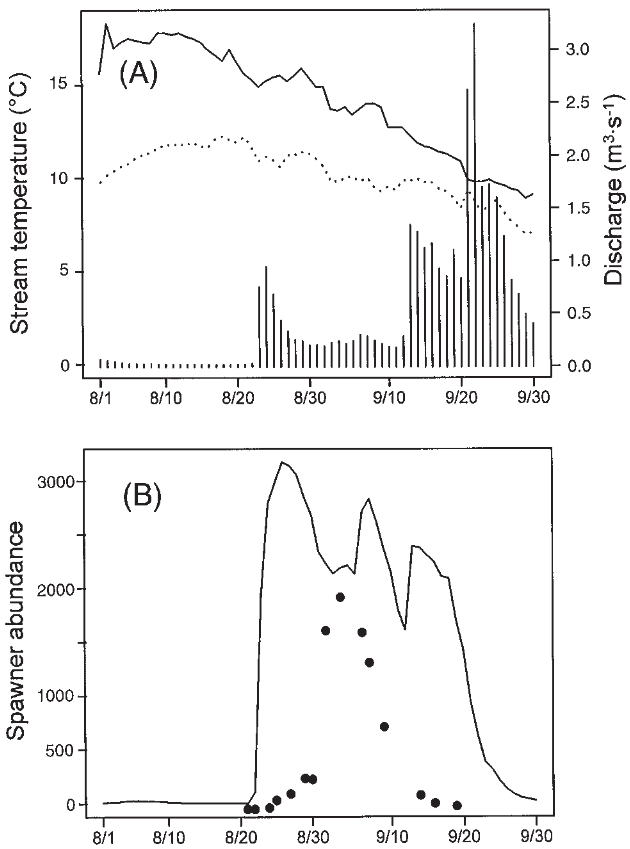
Spawning efficiency E and habitat P are binary responses, for which ordinary linear regression is not applicable because of the limited range (0, 1) and the unequal variances of response variables. Thus, the attributes E and P were analyzed by a logistic regression model that belongs to a family of generalized linear models. For the logistic models, a response variable μ (0, 1) is logit transformed as

$$\eta = \ln(\mu / (1 - \mu))$$

so that the η is mapped onto the real line $[-\infty, \infty]$. The model was fit, and the maximum likelihood estimates of parameters were obtained, by iterative reweighted least squares (McCullagh and Nelder 1983).

The candidate predictor variables for the spawner attributes L, E, and P were (i) Auke Creek temperature T (ii) logarithm of stream discharge ln D, and (iii) spawner abundance S in Auke Creek. One more variable, L, was added as a candidate predictor for the analysis of E, as L and E might have a causal relationship. Auke Creek temperature has been measured every morning by the NMFS since the 1960s. Lake Creek temperature was recorded during the spawning season using an Endeco thermograph but not included as a candidate predictor variable. D was calculated from daily stream gauge readings and observed stream discharges at 10 contrasting gauge heights. S in Auke Creek was estimated from escapement and tagging data by the method described in Appendix 2; visual counting of spawners in Auke Creek was not feasible, unlike in Lake Creek, because of high spawner density and prevalence of deep pools. The actual form of T, D, and S variables was either the 6-day moving average (MV) of daily measurements or simply the daily measurements, depending on the

Fig. 3. Stream temperatures in Auke Creek (solid line) and Lake Creek (broken line) and stream discharge in Auke Creek (bar plot) (A), and pink salmon spawner abundance in Auke Creek (solid line) and in Lake Creek (solid circles) (B) during the 1994 spawning season.



spawner attributes. The moving averages of the first 6 days after Auke Creek entry were used for the analyses of L and E, because these two attributes were probably influenced by average environmental conditions encountered by individual spawners during freshwater residence. In contrast, daily measurements were used for the analysis of habitat P, assuming that whether a fish spawned in Auke Creek or in Lake Creek was determined at the time of, or soon after, the day of immigration. Despite these modifications, the same notations were used for T, D, and S among the different models of spawner attributes.

The selection of predictor variables to be included in regression models was based on a method similar to a stepwise procedure. Starting from a constant model, predictor variables were added to the model one by one. Each time, reduction of deviance was evaluated by a χ^2 test at $\alpha = 0.05$ to decide whether the variable should be retained in the model (McCullagh and Nelder 1983). For the linear regression model of L, the residual sum of squares (RSS) was obtained instead of the deviance, and an F test was used for model comparison instead of a χ^2 test. Residuals in the RSS were scaled by multiplying the square root of the corresponding weight of stream life estimates such that

$$e_i = (w_i)^{1/2}(\ln L_i - \ln \hat{L}_i).$$

To explore the adequacy of model fit and to detect anomalous values, the spawner attributes were plotted against the selected predictor variable for a first-order linear regression model, or partial residuals were plotted against each of the predictor variables for a multiple generalized linear regression model. The partial residuals for predictor variable x_j are

Table 2. Correlation matrix of predictor variables and spawner attributes ($n = 21$ for all combinations).

	T	ln D	S	ln L	logit E
ln D	–0.646*				
S	0.737*	–0.421			
ln L	–0.242	0.754*	–0.154		
logit E	–0.759*	0.249	–0.743*	0.007	
logit P	–0.693*	0.122	–0.552*	–0.230	0.621

*Significant at $p < 0.05$.

$$r_i^j = x_{ij}\hat{\beta}_j + (y_i - \hat{\mu}_i)\,\partial\hat{\eta}_i / \partial\hat{\mu}_i$$

where $\hat{\beta}_j$ is the estimated coefficient for the variable and y_i is the observed proportion, i.e., E_i or P_i (Chambers and Hastie 1992). The term $x_{ij}\hat{\beta}_j$ is thus the jth fitted term, but the individuals of this term were centered such that, when computed for the original data, they average zero. The centering was essential to make standard error plots informative (Chambers and Hastie 1992). All the statistical computation was accomplished using S-PLUS (StatSci 1995).

Results

Auke Creek temperature was about 5°C higher than Lake Creek temperature when pink salmon started the immigration into Auke Creek but decreased almost linearly from 15 to 9°C during the spawning season (Fig. 3A). Stream discharge was negligible until late August when a small freshet on August 23 triggered upstream migration of pink salmon. The estimated spawner abundance in Auke Creek exhibited three modes between late August and late September, whereas spawner counts in Lake Creek appeared to have a single mode in early September (Fig. 3B).

Unlike designed experiments, the candidate predictor variables were correlated, especially T and ln D and T and S ($p < 0.05$; Table 2). Furthermore, T was highly correlated with immigration dates of pink salmon spawners ($r = -0.956$, $p < 0.001$). These correlations make the selection of predictor variables difficult, and empirical consideration may be required during model selection.

Stream life

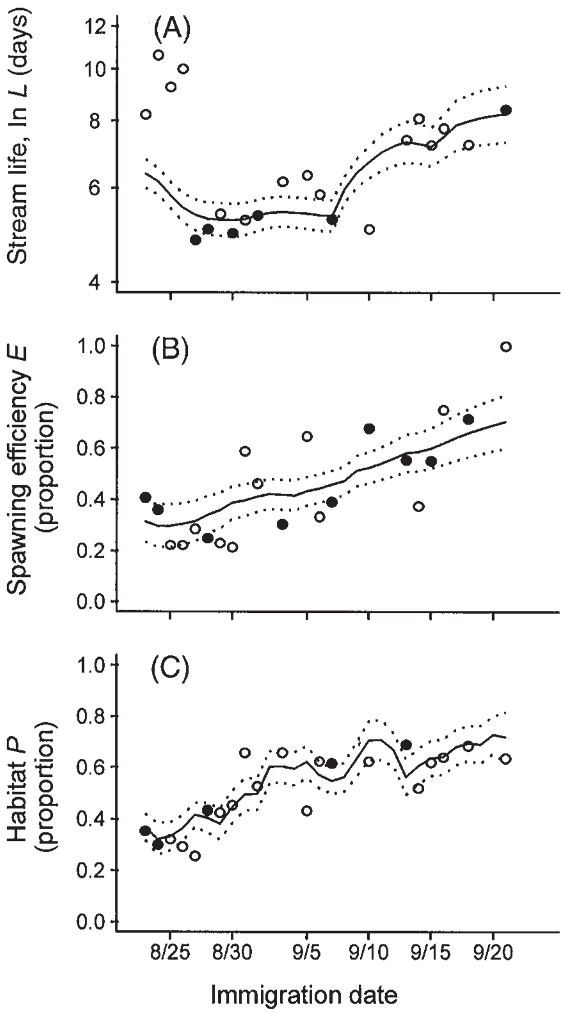
L was 8–10 days at the beginning of the season, decreased to 5–6 days during the midseason, and then rose to about 8 days during the late season (Fig. 4A). The mean L of 584 female pink salmon in Auke Creek was 6.9 days during the 1994 spawning season.

The most parsimonious model relating L to environmental variables contains one predictor variable, ln D, with a positive coefficient ($p < 0.05$), and none of the other variables improved the model fit significantly (Tables 3 and 4). The first four data points of observed L showed consistently higher values than predicted, but weights for these points were all smaller than average (Fig. 4A). Because of the four data points showing longer lives, L appeared to be a dome-shaped function of stream discharge (i.e., the 6-day MV of ln D) rather than a linear function, suggesting that a linear regression may not be appropriate (Fig. 5).

Spawning efficiency

E was particularly low during the early season, so that the majority of the early-run spawners retained more than

Fig. 4. Three attributes of reproductive characteristics plotted against the immigration date of tagged pink salmon. Data points with above and below average weight are marked by solid and open circles, respectively. The weights are the reciprocals of variance, i.e., $1/V(L_i)$ for L, $n_{ei}/E_i(1 - E_i)$ for E, and $M_i/P_i(1 - P_i)$ for P. The predicted line (solid line, see Table 3 for the equation) is accompanied with pointwise 2 × standard error bands (broken lines).



500 eggs when they died in Auke Creek (Fig. 4B). As the season progressed, E steadily increased while stream temperature decreased, which was the only predictor variable in the selected model ($p < 0.05$; Tables 3 and 4). Although the other variables did not appreciably improve the model fit, the observed spawning efficiencies exhibited relatively high variability around the predicted line by the 6-day MV of T (Figs. 4B and 6), suggesting the existence of undetected environmental factors controlling the spawning efficiency of pink salmon. Note that the rate of decrease in the deviance from a constant model (deviance = 57.65) to the selected model (deviance = 28.25) was relatively small (Table 3).

Habitat

The proportion P of daily cohorts spawning in Auke Creek increased from about 0.3 at the beginning to 0.7 at the end of the season (Fig. 4C), indicating that the spawning habitat of pink salmon gradually shifted from Lake Creek to Auke Creek. The estimates of the proportion may be underestimated during the late season, because the higher stream discharges (Fig. 3A) often made the recovery of lost tags impossible. Thus, the actual slope of the increase in Auke Creek spawner proportion may have been even steeper than that observed.

The most significant variable affecting habitat was T ($p < 0.05$), followed by ln D measured on the day of immigration ($p < 0.05$; Tables 3 and 4). The amount of decrease in the deviance was substantial ($p < 0.05$) when ln D was added to a model with a single predictor T (Table 3). Pink salmon spawned in Lake Creek when Auke Creek temperature was higher and when Auke Creek discharge was greater after the temperature effect was eliminated (Table 4, Fig. 7). Partial residual plots indicated that T was a more important predictor for explaining the variation of P than ln D (Fig. 7). There was no abnormal data point in these plots, although the linearity of P against ln D was weak. The estimated standard error was zero at a zero residual because the fitted terms were centered to have a zero mean. Note that the P could be equally well explained by freshwater immigration date of spawners instead of T because of the significant correlation between dates and temperature.

Table 3. Model selection procedures for the three spawner attributes of pink salmon.

Model	df	Deviance[a]	Test[b]	p
Stream life L				
(1) 1	20	0.4620		
(2) ln D	19	0.1575	(2) vs. (1)	<0.001
(3) ln $D + T$	18	0.1545	(3) vs. (2)	0.563
(4) ln $D + S$	18	0.1544	(4) vs. (2)	0.557
Spawning efficiency E				
(1) 1	20	57.65		
(2) T	19	28.25	(2) vs. (1)	<0.001
(3) $T + L$	18	27.92	(3) vs. (2)	0.564
(4) $T + S$	18	26.63	(4) vs. (2)	0.203
(5) T + ln D	18	25.80	(5) vs. (2)	0.117
Habitat P				
(1) 1	20	110.70		
(2) T	19	48.75	(2) vs. (1)	<0.001
(3) $T + S$	18	47.65	(3) vs. (2)	0.294
(4) T + ln D	18	30.31	(4) vs. (2)	<0.001

Note: For each attribute, model 1 is a constant model with no predictor variables.

[a]For the models of L, RSS is given instead of deviance.

[b]F tests were used for the models of L and χ^2 tests were used for those of E and P.

Discussion

Our observation of increasing stream life with immigration date seems to be contrary to our expectation and to other reports of stream life in Pacific salmon in which stream life was longer in early immigrating spawners (Thomason and Jones 1984; Dangel and Jones 1988; English et al. 1992). Increasing stream life tends to desynchronize fry emigration because it separates the spawning events of early and late runs and because embryos spawned early in the season develop faster

Table 4. Parameter estimates for the selected models of spawner attributes.

Attribute	Model	b_0	b_1	b_2
L	(2) $b_0 + b_1 \ln D$	1.97±0.0415	0.202±0.0333	—
E	(2) $b_0 + b_1 T$	3.81±0.752	–0.301±0.0570	—
P	(4) $b_0 + b_1 T + b_2 \ln D$	5.19±0.609	–0.391±0.0449	–0.390±0.0916

Note: Values are given as means ± standard error. See Table 3 for model numbers.

Fig. 5. Observed and predicted stream life (ln L) plotted against stream discharge (ln D). Data points with above and below average weight are marked by solid and open circles, respectively. The predicted line (solid line) is accompanied with pointwise 2SE limits (broken lines). See Table 3 and Fig. 4 for the equations of the predicted line and the weight, respectively.

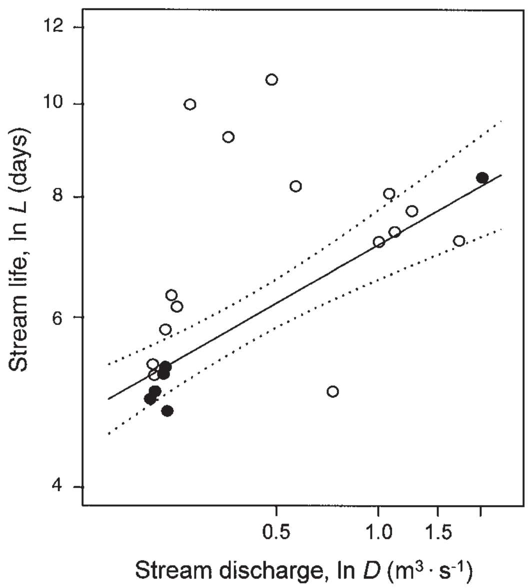
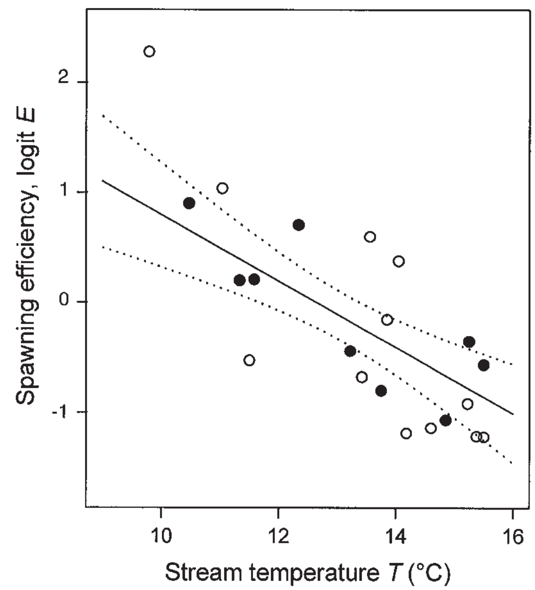


Fig. 6. Observed and predicted spawning efficiency (logit E) plotted against stream temperature (T). Data points with above and below average weight are marked by solid and open circles, respectively. The predicted line (solid line) is accompanied with pointwise 2 × standard error bands (broken lines). See Table 3 and Fig. 4 for the equations of the predicted line and the weight, respectively.



under higher incubation temperature. However, it should be recalled that the stream life in this analysis applies only to Auke Creek spawners and does not include Lake Creek spawners. Apparently, most spawners counted in Lake Creek in early September originated from the first run of pink salmon observed in Auke Creek in late August (Fig. 3B), because the majority of these pink salmon spawned in Lake Creek. This indicates that Lake Creek entry by the first-run spawners was delayed more than a week and that these spawners actually had a fairly long stream life.

Stream discharge was the predictor that best explained the variation in stream life, although the relationship may not be linear; female pink salmon lived longer when discharge was moderate. Despite a severe freshet during late September, however, the late-run spawners apparently lived longer than the average stream life (Figs. 3A and 4A). Low discharge, on the other hand, probably delayed the entry of spawners into fresh water and decreased the oxygen supply to them, thus shortening their lives.

The shorter stream lives of female pink salmon were accompanied by a large prespawning mortality caused by high stream temperatures above 15°C in late August. The variation in spawning efficiency was best explained by stream temperature, but the higher spawning efficiency later in the season may have resulted from a relatively longer stream life of late-spawning fish (Fig. 4A). Stream life, though it was included as a candidate predictor variable, was not selected in the model largely because of the first four observations of exceptionally long stream lives that were against the trend of spawning efficiency. Approximately 70% of the early-run spawners retained more than 500 eggs (Fig. 4B), which is abnormal in light of typical egg retentions reported for this species (less than 5% of total fecundity; McNeil 1968; Heard 1978). Our observation in 1994 may have been anomalous, but similar sustained high temperatures in Auke Creek during late August have been observed in other recent years (e.g., 1989, 1992, 1993; data on file, Auke Bay Fisheries Laboratory, 13305 Glacier Highway, Juneau, AK 99801, U.S.A.). Also, similar large-scale mortalities of prespawning pink salmon have been reported from several streams in southeastern Alaska during drought and high temperature (Murphy 1985).

An effect of spawner abundance on habitat, or the proportion of female pink salmon spawning in Auke Creek, was not observed. In Sashin Creek, southeastern Alaska, higher spawner abundance has been reported to cause pink salmon to migrate farther upstream and seek less crowded spawning grounds (Merrell 1962; McNeil 1966, 1968; Heard 1978).

Merrell (1962) and McNeil (1966, 1968) observed that pink salmon tended to spawn in the lower area of Sashin Creek in years when the spawner abundance was low, while in years of high spawner abundance a large number of spawners intensively used the upper area of the creek as well as the lower area.

The most significant predictor variable of habitat of the 1994 pink salmon was stream temperature. Pink salmon spawned in the cooler streamflow of Lake Creek when Auke Creek was warm. However, because Auke Creek temperatures and immigration dates are indistinguishable in their effects on habitat because of their strong correlation, the habitat could have been equally well explained by immigration date instead of stream temperature. It is thus uncertain whether the shift of habitat is related to a behavioral response to environmental factors showing a linear trend such as stream temperature or is a genetic trait specific to the different runs of pink salmon. In this regard it is worth noting that variation in run timing has been shown to have a significant basis in genetic variation in odd-year pink salmon in the Auke Lake system (Smoker et al.,[2] unpublished).

The habitat shift from upstream to downstream during a spawning season may or may not be typical for Auke Creek, but it would not be peculiar to the pink salmon population in the Auke Lake system. It has been observed for other populations of pink salmon and even for other salmonid species (Briggs 1955; McNeil 1966, 1968; Saunders 1967; Burger et al. 1985; Fukushima 1994). Briggs (1955) hypothesized that in anadromous or potamodromous fishes the earliest arrivals in a particular spawning tributary will travel to the farthest reaches of the acceptable breeding area, the later arrivals occupying territories closer to the mouth of the stream. The consequence of such a migratory trait would be directly related to different developmental rates of embryos spawned in different temperature regimes. Upstream water temperatures are lower than downstream temperatures in most stream systems and especially so in lacustrine systems (Burger et al. 1985). In Auke Creek, for example, despite the higher stream temperature encountered by the early-run spawners when they first entered fresh water, their embryos actually started development at lower incubation temperatures in the inlet Lake Creek than the late-run embryos spawned in the outlet Auke Creek (Fig. 3A).

No matter whether it was due to environmental factors or a genetic trait, the habitat shift observed in the Auke Lake system in 1994 would have contributed to synchronous fry outmigration in the spring of 1995. It is highly plausible that the similar time spans of adult immigration and fry emigration of pink salmon during the last 15 years (Fig. 2) were also attributable to a consistent pattern of habitat shift in which early-run pink salmon spawned in relatively cooler Lake Creek and late-run pink salmon spawned in warmer Auke Creek.

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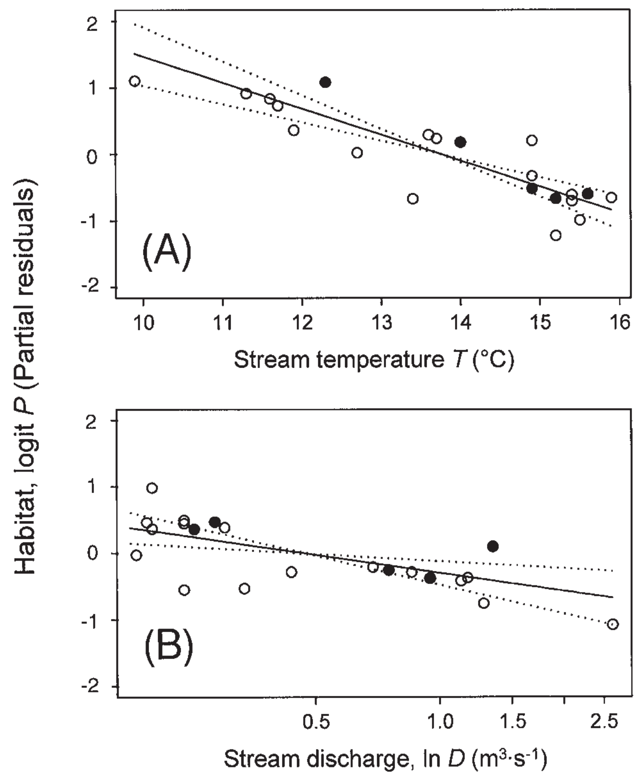
[2] Presented as "Genetic variation in timing of anadromous migration within a spawning season in a population of pink salmon" by W.W. Smoker, A.J. Gharrett, and M.S. Stekoll to the Internation Symposium on Biological Interactions of Enhanced and Wild Salmonids, June 1991, Nanaimo, B.C.

Fig. 7. Partial residuals of habitat (logit *P*) for stream temperature (*T*) (A) and for stream discharge (ln *D*) (B) plotted against respective predictor variables. Data points with above and below average weight are marked by solid and open circles, respectively. The predicted line (solid line) is accompanied with pointwise 2 × standard error bands (broken lines). See Table 3 for the coefficient of the predicted line and Fig. 4 for the equation of the weight.



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Appendix 1

Summary of the 1994 tagging study, showing daily escapement of pink salmon, the number of tagged pink salmon, the number of tag recoveries in Auke Creek, stream life L, its variance $V(L)$, sample size n for the stream life measurement, the number of carcasses with less than 500-egg retention (few), those with more than 500 retention (many), and the sample size n_e (few + many) for the egg retention measurement.

				Stream life			Egg retention		
Tag date	Escapement	No. tagged	No. recovered	L (days)	V(L)	n	Few	Many	n_e
Aug. 23	5195	212	75	8.2	11.22	72	22	32	54
Aug. 24	2830	113	34	10.6	18.78	31	9	16	25
Aug. 25	786	50	16	9.3	13.53	16	2	7	9
Aug. 26	636	41	12	10.0	8.73	12	2	7	9
Aug. 27	310	39	10	4.8	1.07	10	2	5	7
Aug. 28	312	76	33	5.0	1.78	33	7	21	28
Aug. 29	298	47	20	5.4	2.69	19	3	10	13
Aug. 30	282	44	20	4.9	1.06	17	3	11	14
Aug. 31	349	38	25	5.2	2.18	22	10	7	17
Sept. 1	403	36	19	5.3	0.47	18	6	7	13
Sept. 2	543	—	—	—	—	—	—	—	—
Sept. 3	666	41	27	6.2	2.81	25	7	16	23
Sept. 4	575	—	—	—	—	—	—	—	—
Sept. 5	665	44	19	6.3	4.47	18	11	6	17
Sept. 6	1466	40	25	5.8	2.67	24	6	12	18
Sept. 7	803	94	58	5.2	1.57	53	18	28	46
Sept. 8	186	—	—	—	—	—	—	—	—
Sept. 9	310	—	—	—	—	—	—	—	—
Sept. 10	282	56	35	5.0	2.03	33	21	10	31
Sept. 11	245	—	—	—	—	—	—	—	—

Appendix 1 (*concluded*).

				Stream life			Egg retention		
Tag date	Escapement	No. tagged	No. recovered	*L* (days)	V(*L*)	*n*	Few	Many	n_e
Sept. 12	525	—	—	—	—	—	—	—	—
Sept. 13	1890	100	69	7.4	4.06	69	36	29	65
Sept. 14	571	50	26	8.1	2.41	25	9	15	24
Sept. 15	220	50	31	7.2	5.06	30	16	13	29
Sept. 16	165	25	16	7.8	3.80	16	12	4	16
Sept. 17	54	—	—	—	—	—	—	—	—
Sept. 18	214	54	37	7.2	3.43	36	25	10	35
Sept. 19	43	—	—	—	—	—	—	—	—
Sept. 20	25	—	—	—	—	—	—	—	—
Sept. 21	22	11	7	8.4	0.80	5	4	0	4

Appendix 2

Calculation of daily spawner abundance *S*

Let N_i be the pink salmon escapement on the *i*th day, M_i be the number of pink salmon tagged on the *i*th day, m_{ij} be the number of tags originating from M_i and recovered on the *j*th day, and

$m_{i.} = \sum_{j=i}^{\infty} m_{ij}$, i.e., the total number of tags recovered from M_i

The estimated number of pink salmon that entered on the *i*th day and spawned in Auke Creek becomes

$$\hat{N}_{Ai} = \frac{m_{i.}}{M_i} N_i$$

and $N_i - N_{Ai}$ fish spawned in Lake Creek. The estimate of the survival rate of Auke Creek spawners from the *i*th day to the *t*th day is given by

$$\hat{\phi}_{it} = \frac{m_{i.} - \sum_{j=i}^{t} m_{ij}}{m_i}$$

Thus, the estimated number of Auke Creek spawners that entered on the *i*th day and were still alive on the *t*th day is

$$\hat{S}_{it} = \hat{N}_{Ai} \cdot \hat{\phi}_{it} = \frac{m_i}{M_i} N_i \frac{m_{i.} - \sum_{j=i}^{t} m_{ij}}{m_{i.}}$$

$$= \frac{N_i}{M_i}\left(m_{i.} - \sum_{j=i}^{t} m_{ij}\right)$$

Finally, the estimate of Auke Creek spawner abundance on the *t*th day is obtained as

$$\hat{S}_t = \sum_{i=1}^{t} \hat{S}_{it} = \sum_{i=1}^{t} \frac{N_i}{M_i}\left(m_{i.} - \sum_{j=i}^{t} m_{ij}\right)$$