Stream Temperatures and Inter-Annual Variability in the Emigration Timing of Coho Salmon (*Oncorhynchus kisutch*) Smolts and Fry and Chum Salmon (*O. Keta*) Fry from Carnation Creek, British Columbia[1]

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Variability in average stream temperatures between peak spawning and fry emergence accounted for 82 and 77% of the variance in the median emigration date of fry of chum (*Oncorhynchus keta*) and coho salmon (*O. kisutch*), respectively, over a 9 to 10-yr period. The modeled relationships were indistinguishable from laboratory models that predicted time to maximum alevin wet weight. Variability in stream temperatures during the spring accounted for 60% of the variability in the median date of coho smolt emigration. As stream temperatures increased, the predicted thermal summations required for emigration were nearly constant for coho salmon fry, increased moderately for chum salmon fry and increased strongly for coho salmon smolts. The duration of the emigration period also differed between the groups: 50% of the chum salmon fry emigrated over a 1-wk period compared with a 2- to 3-wk period for coho salmon fry and smolts. We speculate that the emigration timing — temperature relationships and timing of adult spawning represent adaptations for synchronizing emigration with "windows of opportunity" in the ocean or stream. The windows are of different widths and levels of predictability for coho and chum salmon fry and coho salmon smolts.

La variabilité de la température moyenne du courant entre la période maximale de fraie et l'émergence des alevins comptait respectivement pour 82 et 77 % de la variance de la date de migration des alevins de saumon kéta (*Oncorhynchus keta*) et de saumon coho (*O. kisutch*) au cours d'une période de 9 à 10 ans. Les rapports modélisés étaient indistinguables des modèles de laboratoire qui prédisaient la période nécessaire pour que les alevins atteignent leur poids frais maximal. La variabilité de la température du courant au printemps comptait pour 60 % de la variabilité de la date médiane de migration des smolts de saumon coho. A mesure qu'augmentait la température, les sommations thermiques prévues pour la coho, augmentaient de façon modérée pour les alevins de saumon kéta et augmentaient fortement pour les smolts de saumon coho. La durée de migration différait également d'un groupe à l'autre : 50 % des alevins de saumon kéta migrent sur une période de 1 semaine comparativement à une période de 2 à 3 sem. pour les alevins et les smolts de saumon coho. Nous formulons l'hypothèse que les rapports entre le moment de la migration et la température et le moment du frai à l'âge adulte représentent des adaptations à une migration synchronisée en fonction de « fenêtres spécifiques » dans l'océan ou les cours d'eau. La largeur des fenêtres varie de même que le niveau de prévision pour les alevins des saumons coho et kéta et les smolts de saumon coho.

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Two periods in the lives of juvenile Pacific salmon (*Oncorhynchus* spp.) involve major habitat transitions that are particularly hazardous. Emergence of the fry and the initiation of feeding involves leaving secure, low energy environments in the interstices of stream bed gravels and entering the high energy environment of the stream. Among populations of coho salmon (*O. kisutch*), where juveniles spend a year or more in fresh water, 40–60% of the emerging fry die in the month or two following emergence (Au 1972; Hartman and Scrivener 1986). A second period of high mortality follows the entry of smolts into the ocean (Hunter 1959; Parker 1968; Healey 1982; Murphy et al. 1988). Although the specific mortality agents are unknown (Healey 1982), predation by both piscivorous fishes and marine birds probably accounts for most of the mortality (Godin 1981). In coastal streams, the juveniles of chum salmon (*O. keta*) enter the ocean very soon after emergence and must make both transitions at roughly the same time. Mortalities of $40\% \cdot d^{-1}$ have been observed at this time (Bax 1983).

Entering a new environment at a specific time is probably adaptive, minimizing predation risk and maximizing individual growth (Bams 1969; Walters et al. 1978; Godin 1981; Miller and Brannon 1981; Riddell and Leggett 1981; Murphy et al. 1988), and must involve physiological and/or behavioural control of timing. Although it has been well established in many

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fish species, including salmonids, that emergence and emigration timing are affected by temperature, several aspects of the temperature dependencies have received little critical attention. First, there have been very few demonstrations that laboratory models relating the emergence timing of fry to temperature are applicable to populations in the field. For example, the model we use in this study (time to maximum alevin wet weight; Rombough 1985) has been proposed as a reliable predictor of emergence and emigration timing in wild systems (Bams 1970; Heming 1982), but never tested. Second, examinations of the role of temperature in influencing the emigration timing of salmon smolts (Foerster 1937; Solomon 1978; Clarke et al. 1981; Jonsson and Ruud-Hansen 1985) are not well integrated into our current understanding of the smoltification process. Third, comparisons of the responses of emergence or emigration timing to temperature change among more than one species or life-history stage of Pacific salmon in a single system are lacking. And finally, there is no well defined conceptual framework within which such comparisons can be interpreted.

Our objectives in this study were: (1) to present a 17-yr time series of emergence and emigration timing and temperature for the juveniles of two species of Pacific salmon; (2) to demonstrate that temperature variation drives variation in emergence and emigration timing; (3) to test a specific temperature-dependent model of emergence timing in a wild system; (4) to examine the effects of temperature variation on inter-annual variability in the emigration timing of coho salmon smolts within the context of recent laboratory studies relating photoperiod and the initiation of the smolt transformation; and (5) to compare the temperature dependencies of emergence and emigration timing of chum and coho salmon fry and coho salmon smolts using a simple conceptual model.

Methods

Study Site

Carnation Creek lies on the southeast side of Barkley Sound, Vancouver Island. The stream drains an area of ≈10 km^2 and is 8 km long, of which the lower 3.1 km is accessible to anadromous salmonids. The physical and biological characteristics of the stream have been described in detail elsewhere (Hetherington 1982; Hartman and Holtby 1982; Hartman et al. 1987).

Biological Data

Much of the biological data used in our analyses has been summarized by Andersen (1983, 1984, 1985, 1987).

Characteristics of adult spawner immigration are important since the timing and temporal pattern of egg deposition, fry emergence, and emigration are directly related. The run timing of adult spawners was determined from fence counts for coho salmon, beginning in 1972 (Holtby et al. 1984), and by regular streamside surveys below the counting fence for chum salmon beginning in 1970 (Holtby and Scrivener 1989). Adult enumeration was carried out from the beginning of September until early March. All coho salmon adults were enumerated. Most of the chum salmon spawn in the estuary below the counting fence (73–95%), but the area is small (≈200 m by 10 m), shallow (<1 m), and devoid of cover, enabling accurate counts of spawners.

Coho salmon smolts and fry of both coho and chum salmon were enumerated at a fish-counting fence located 75 m upstream of the mean high tide mark. Juveniles were trapped from early-March through late-August during each year from 1971. The fork lengths (FL) of all coho smolts were measured to the nearest millimetre. Scale ages of coho smolts were determined at 7–10 d intervals and the scale age–FL relationship was then applied to age smolts emigrating within that period. In the fall of 1983 no chum salmon spawned above the fence. Fry emigration timing during that year was provided by 12 emergence traps positioned below the fence (Scrivener 1988).

The trapping efficiency of the fence for emigrant juveniles is 100% in all but the most severe of spring freshets, of which there are usually several each year. Partial operation of the fence was possible at all flow levels however, and smolt and fry counts during freshets indicated that few fish emigrate during peak flows (B. C. Andersen, Pacific Biological Station, Nanaimo, pers. comm.). Emigrant numbers during freshets were estimated by expanding the partial catches by the proportion of the total discharge screened. In most years more than 95% of emigrants were actually counted.

In this study we equate the observed emigration timing of fry through the fence with emergence timing. Chum fry appeared at the counting fence at the same time as they appeared in emergence traps placed over spawning gravels below the fence. Comparisons of the size distributions of emigrating fry passing the counting fence with those caught in emergence traps below the fence indicated that few, if any, of the fry remained in the stream to feed after emergence: this refutes Mason's (1974) observations. Similarly, coho fry were observed at the fence at the same time as they first appeared in the stream and were of the same size (Hartman et al. 1982). On average, 54% of the coho fry emerging passed the counting fence, regardless of total emergence (Holtby 1988). These observations strongly suggest that large numbers of coho salmon fry are physically displaced from the stream soon after emergence (Scrivener and Andersen 1984), and that the timing of their movements can be used as an approximate measure of emergence timing.

Stream Temperatures

Water temperatures in Carnation Creek were recorded continuously by a Lambrecht 256C thermograph at the main hydrological weir, located 350 m upstream of the counting fence. The thermograph was calibrated weekly using a mercury thermometer. Recorder tracings were digitized at intervals ranging upward from 15 min, as required to capture the shape of the thermal tracing. During digitizing, the records were corrected for instrument drift (both temperature and time). Mean daily temperatures were then interpolated from the digitally-stored thermal trace. All of the mean temperatures used in this study were the means of daily means. Between late 1975 and early 1981, 41% of the total watershed was clear-cut logged, including much of the streambank in the lower sections of the stream (Dryburgh 1982). Stream-side logging sufficient to alter stream temperatures during the winter and spring did not begin until the winter of 1976 (Holtby 1988).

Temperature Models

We used a semi-logarithmic model:

$$(1) \quad \log t = a + b \times T,$$

to relate t, the elapsed time between some predetermined date and the median date of emigration, to T, the average temperature over the same period. The functions used to describe relationships between development and emigration timing and temperature are empirical rather than theoretical (Crisp 1981). For that reason, small differences in fit between the many alternative models are probably meaningless, especially in a field study where there are many uncontrolled variables.

We did not fit the temperature models to all available data because the relationships between temperature and emigration timing can change after large temperature perturbations (Lannan 1980) such as those that followed logging (Holtby 1988). Altered temperature relationships associated with logging would not have been detectable at Carnation Creek until the progeny of the first cohorts affected by the temperature perturbations emigrated. Consequently, our models of emigration timing were based on the 9 yr (for coho salmon) or 10 yr (for chum salmon) in the prelogging and immediate postlogging period. We compared observed emigration times in the remaining postlogging period with those predicted by our models in order to test for changes in the thermal requirements for emigration of the type described by Lannan (1980).

The temperature averaging period for chum salmon fry began on the date that 50% of the adults passed upstream through the counting fence and ended on the median date of downstream fry emigration. In 1983 no female chum salmon passed upstream and the averaging period commenced on the date of peak live spawner counts on the spawning grounds below the fence and ended on the date of peak fry numbers in the emergence traps. We were uncertain of when coho salmon spawned after entering the stream. Consequently, we averaged temperatures over five periods with starting dates of the median day of adult immigration, 2, 3, and 4 wk after that date and 3 wk after the overall mean immigration date. All periods ended with the median date of downstream fry emigration. To delimit the appropriate temperature averaging period for coho smolt emigration, we averaged temperatures over 18 periods, with starting dates varying from January 1 to April 15 at 1-wk intervals. All periods ended on the median date of smolt emigration. The averaging periods selected were the ones for which the correlations between temperature and median emigration date were greatest.

Two other analyses were used to strengthen the correlative evidence that emigration timing was mainly dependent on temperature. First, other factors that are known to affect fry emergence (Bams 1969; Koski 1975; Everest et al. 1987) and smolt emigration (Grau 1981; Jonsson and Ruud-Hansen 1985) were added to our temperature models in an attempt to improve predictability of emigration timing. Second, our models of fry emigration were compared with two unpublished models relating temperature (T) and time to maximum alevin wet weight (t_{MAWW}; P. Rombough, Zoology Dept., Brandon University, Brandon, Manitoba, pers. comm.):

$$(2)\quad \text{chum salmon } \log t_{\mathrm{MAWW}} = 5.6677 - 0.1008 \times T (n=9; r^2=0.96)$$

$$(3)\quad \text{coho salmon } \log t_{\mathrm{MAWW}} = 5.7467 - 0.1355 \times T (n=11; r^2=0.98).$$

Eggs of both species came from the Big Qualicum River, B.C., and were incubated in the laboratory where all factors but temperature were controlled. We were unable to locate any relationships between the smolt transformation rate and temperature.

TABLE 1. Adult immigration timing data. Unless otherwise indicated the dates shown are for fence passage. The coho data includes jacks. Dates are encoded as month. day. The arrows indicate the first adult returns influenced by logging.

	Median date of stream entry	
Year	Chum salmon	Coho salmon
1970	10.22[a]	—[b]
1971	11.5[a]	—[b]
1972	11.7	11.4
1973	10.24	10.20
1974	11.9	11.9
1975	10.25	10.18
1976	10.30	10.30
1977	10.29	10.29
1978	10.28	10.28
1979	10.27	→ 10.27
1980	→ 10.25	10.27
1981	10.31	10.31
1982	10.23	10.24
1983	10.22[1]	10.23
1984	10.28	10.13
1985	10.26	10.19
1986	11.1	11.1

[a] Determined from spawning ground surveys.

[b] No fence or survey data are available.

Comparison of Temperature Relationships

To better characterize species and life-stage responses to temperature variability, we used our models to calculate median emigration dates for a range of stream temperatures derived from a reconstructed 52-yr temperature time series for Carnation Creek in a natural state (Holtby 1988). Emigration dates were calculated for temperature values of the historical minimum, the tenth, twenty-fifth, fiftieth, seventy-fifth and ninetieth percentiles and the historical maximum. Emigration dates predicted by the temperature models were also compared with dates calculated assuming either temperature independence or a constant thermal requirement for the three life-stage groups. For temperature independence, the emigration date was the date predicted by the temperature model at the historical median temperature. To calculate the emigration dates assuming a constant thermal requirement, we first calculated the product of the historical median temperature and the elapsed time to emigration predicted by the temperature model at that temperature. The time to emigration at each temperature in the historical range was calculated by dividing that product by the particular temperature.

Results

Adult Run Timing

The overall median date of stream entry was October 28 for both species. For chum salmon, the overall range of median entry dates was 18 d, but in 14 of 17 yr the median date was within 7 d of October 28 (Table 1). In contrast, the overall range in median entry date for coho salmon was 26 d and in only 9 of 15 yr was the median date within 7 d of the overall median (Table 1). The greater overall range of entry dates of coho salmon was due to several years in which 50% of the adults entered the stream as much as 2 wk before the overall median date (Table 1). Annual deviations from October 28 for both species were significantly correlated ($r=0.711$, $p<0.01$, $n=15$; Fig. 1). The entry of coho salmon was dependent on stream flows in all years (Holtby et al. 1984), but for chum salmon, that dependence was probably valid only if the first fall

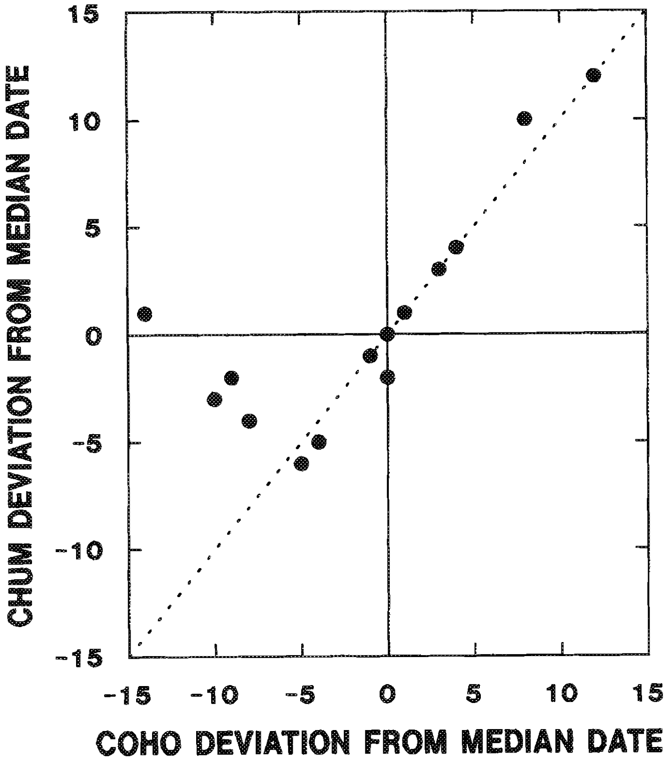

FIG. 1. Deviations, in days, from overall study median spawning dates for chum salmon versus coho salmon.

storms of the year occurred after October 31. Adult chum salmon did not enter the stream in mid-October in years when stream discharges were sufficient for adult coho salmon to do so (Fig. 1).

Although the median dates of arrival were virtually identical for the two species, within year dispersions were not. In most years, 50% or more of the adult chum salmon arrived at the stream within a very short period, often the same day (B. C. Andersen, Pacific Biological Station, Nanaimo, B.C., pers. comm.; Scrivener 1988). Very few adult chum salmon were observed before mid-October or after mid-November. In contrast, the arrival of adult coho salmon was protracted, with the first fish observed in mid-September and the last fish usually seen in mid-December. Adult coho salmon have been observed entering the stream as late as mid-January (Holtby et al. 1984). Similar behaviour has been described in other streams (e.g. Moring and Lantz 1975).

Timing of Spawning

From observations of spawner behaviour we knew that spawning by the bulk of the chum salmon commenced within a day or two of entry into the stream (Scrivener 1988) and we assumed that this was also true of the spawners that passed the fence. In contrast, most of the coho salmon adults passed over the fence were not in spawning colours and the ovaries of females were firm. Scattered observations of fish in the stream suggested that spawning occurred several weeks after stream entry.

Emigration of Chum Salmon Fry

Prior to clear-cut logging, chum salmon fry were usually the first to emigrate, with the median date ranging between April 23 and May 12 (Table 2). Winter and spring temperatures increased as a result of logging, and by the spring of 1981 the temperature perturbation was approximately 1–2°C (Holtby 1988). Associated with those temperature increases emigration timing of chum fry was advanced by as much as 6 wk (Table 2).

The median dates of emigration timing for chum salmon fry were highly correlated with average stream temperatures for the period between egg deposition and fry emergence (Table 3; Fig. 2A). In the 1971–80 period, average stream temperatures during egg incubation accounted for 82.4% of the variance in the elapsed time between spawning and fry emigration (Table 3). The slope of the regression (b), was smaller when all 17 yr of data were used, but not significantly so ($t=1.10$, $df=23$, $p>0.2$), and thus, although thermal requirements for emigration increased after the temperature perturbations of logging, the increases were not statistically significant.

For the period 1981–87, the temperature model predicted the median emigration date to within 10 d in all 7 yr and the 95% confidence interval for predicted values encompassed all observations (Fig. 2A). However, the fry consistently emigrated later than predicted.

The relationship between temperature and time to maximum alevin wet weight (t_{MAWW}; equation 2) was statistically indistinguishable from the fitted temperature model and predicted emigration time to within 3 d in most years from 1971–80 and to within 10 d in all years from 1971–87 (Fig. 2A).

Coho Salmon Fry

Coho salmon fry emigrated after chum salmon fry (sometimes 2 wk later; Table 2) from 1971 to 1981. Thereafter, coho salmon fry tended to emigrate before the chum salmon fry.

For the period 1971–79, the number of days between the median date of adult entry and the median date of fry emigration was not significantly correlated with stream temperatures averaged over the same period ($r=0.568$, $n=9$, $p>0.05$), or with periods beginning 2, 3, or 4 wk after the adult immigration date ($r=0.629$, 0.650, 0.659, respectively, $n=9$ and $p>0.05$ for all). However, large amounts of variance could be accounted for by assuming a fixed date in mid to late November to start temperature averaging. Because scattered observations indicated that coho spawned 2–4 wk after entering the stream, we began the averaging period on November 18, 3 wk after the overall median date of spawner entry to the stream. The average temperature over that period accounted for 76.9% of the variance in days elapsed between November 18 and the median date of fry emigration, for the years 1971–79, (Table 3). Expanding the data to include all of the study years led to decreased levels of explained variance but no significant change in the slope of the regression ($t=0.53$, $df=22$, $p>0.5$). The t_{MAWW} model (equation 3) was indistinguishable from the fitted temperature model (Fig. 2B).

In the period 1980–87, the observed median emigration dates were within 4 d of those predicted in 5 of 8 yr, and all but two of the observed dates were within the 95% confidence interval (Fig. 2B). There was no consistent tendency of the model to over- or underestimate emigration dates.

Coho Salmon Smolts

The median date of coho salmon smolt emigration ranged from April 24 to May 15 over the 17-yr study, which was the least variable emigration date of the three groups (Table 2). The

TABLE 2. Juvenile emigration timing data. The inter-quartile range ($t50$) and the 10 to 90% range ($t80$) in days are shown for fry and smolts with both age groups combined.

	Coho salmon smolts					Coho salmon fry			Chum salmon fry		
	Median date (mo. d)										
Year	1^+	2^+	Both	$t50$	$t80$	Median date (mo. d)	$t50$	$t80$	Median date (mo. d)	$t50$	$t80$
1971	5.15	5.15	5.15	14	47	5.14	17	52	5.1	11	26
1972	5.2	5.5	5.3	31	66	5.18	30	51	5.12	9	22
1973	5.8	5.7	5.8	17	36	5.6	20	38	5.5	7	14
1974	5.8	5.11	5.9	28	55	5.11	30	51	4.28	10	17
1975	5.6	5.12	5.9	17	36	4.26	10	19	5.1	18	29
1976	5.9	5.10	5.9	22	37	5.16	27	42	4.23	14	34
1977	5.3	5.4	5.3	17	38	4.9	7	26	4.7	6	14
Logging begun											
1978	5.1	4.29	5.1	23	48	4.14	11	24	4.12	8	15
1979	4.29	4.29	4.29	18	33	4.22	19	28	4.22	5	9
Parents affected by temperature perturbations									4.5	2	5
1980	4.30	4.28	4.30	15	31	4.14	9	22			
1981	5.5	4.30	5.5	22	45	3.23	7	24	3.19	8	13
1982	5.6	5.4	5.6	14	32	4.11	13	17	4.16	3	9
1983	4.25	4.19	4.24	18	38	3.27	15	25	3.24	5	9
1984	5.6	4.27	5.6	22	44	3.19	22	38	4.8	10	18[a]
1985	5.3	5.1	5.3	12	25	4.11	19	29	4.24	11	16
1986	4.27	5.2	4.27	26	41	4.16	17	23	4.16	6	10
1987	4.26	4.25	4.26	15	33	4.6	7	11	4.7	5	18

[a] Data from estuary emergence traps.

TABLE 3. Temperature models for emigration timing in the form of $\log t = a + b \times T$, where t is the number of days between either D50A, the median date of adult entry or a fixed date (mo. d) and D50F, the median date of fry emigration, or t is the number of days between a fixed date and D50S, the median date of smolt emigration. T is the average temperature over the same period. All regressions were significant at the 0.01 level or better.

Species/period	Averaging period	n	a	b	r^2_{adj}
Chum salmon fry					
1971–80	D50A to D50F	10	5.655	−0.0966	0.824
1971–87	D50A to D50F	17	5.573	−0.0787	0.878
Coho salmon fry					
1971–79	11.18 to D50F	9	5.773	−0.142	0.769
1971–87	11.18 to D50F	17	5.640	−0.118	0.667
Coho salmon smolts					
1971–79	2.25 to D50S	9	4.569	−0.0605	0.600
1971–87	2.25 to D50S	17	4.503	−0.0475	0.475

date of coho salmon smolt emigration was also the least affected by the logging perturbation, advancing by a maximum of 2 wk compared with fry emigration advancement of 7 wk. There were no consistent differences in the emigration timing of the two age groups of coho salmon smolts (Table 2). In the years prior to 1978, when there were roughly equal numbers of the two age groups, the older and larger fish did tend to emigrate later than the younger group. Beginning in 1978 there were progressively fewer 2-yr old smolts and a tendency for those smolts to migrate earlier than the increasingly abundant 1-yr old smolts. The significance of the differences in migration timing of the two age groups are unknown, and while they may represent an age or size effect on emigration timing, they may also be an artifact of estimating emigration timing for a progressively less abundant age-group. For the remainder of this paper we have combined the two age groups of smolts and have calculated the timing statistics from the daily pooled numbers of emigrants.

Of the 18 averaging periods considered for the temperature model, the highest correlations were for the period starting February 25 (Fig. 3). The strengths of the correlations were not much different with starting times that varied by several weeks either side of February 25, but decreased with earlier and particularly with later dates. The average temperature from February 25 to the median date of smolt emigration explained 60.0% of the variation in the elapsed time to smolt emigration (Table 3). The amount of explained variance fell to 47.5% when the entire study period was included (Table 3) and the slope was smaller, but not significantly so ($t = -.56$, $df = 22$, $p > 0.5$).

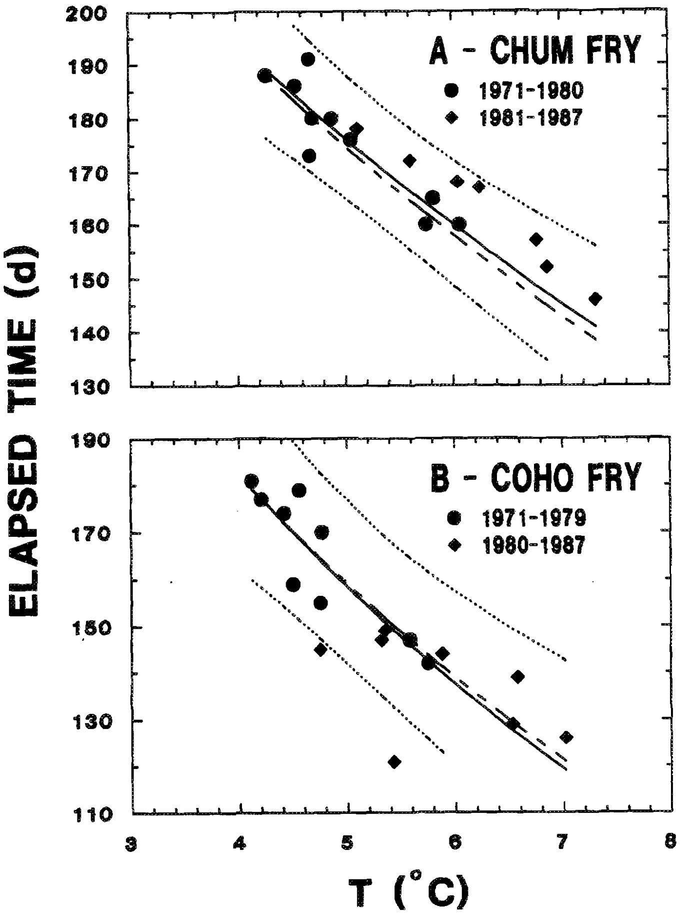

FIG. 2. Observed median date of (A) chum and (B) coho salmon fry emigration versus average stream temperatures over the period D50A–D50F (notation per Table 3). Model fitted to the data (______). 95% confidence interval for predicted dates (····). t_{MAWW} model predictions (— — —).

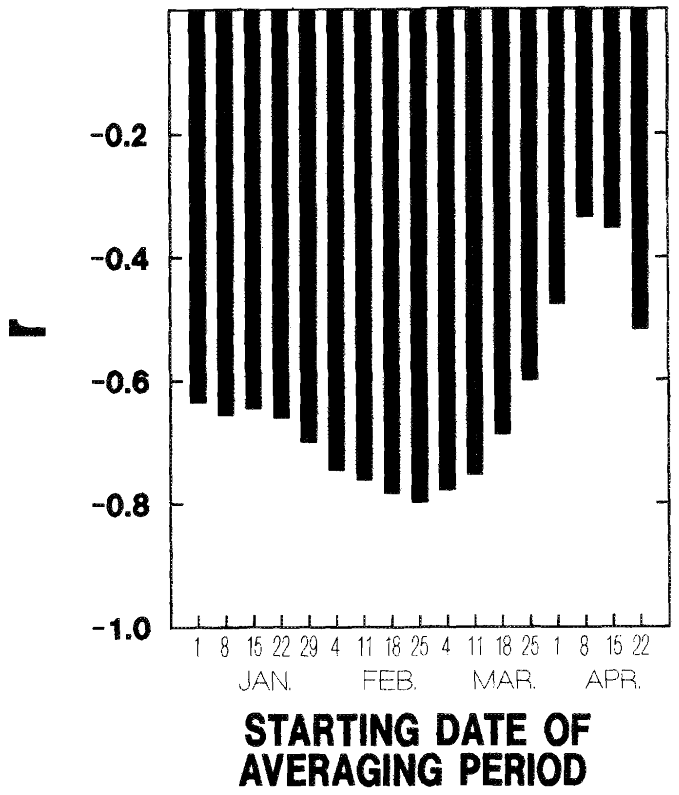

FIG. 3. Correlations between stream temperatures and median date of coho salmon smolt emigration. The temperature averaging periods began on the indicated date and ended on the median date of smolt emigration.

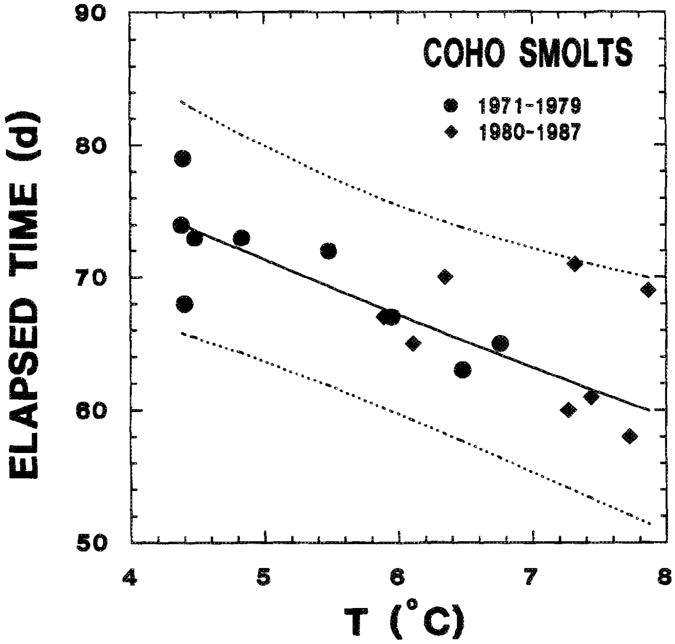

FIG. 4. Observed median date of coho salmon smolt emigration versus average stream temperatures over the period 2.25–D50S (notation per Table 3). Model fitted to the data (______). 95% confidence interval for predicted dates (····).

Predicted emigration dates were within 2 d of those observed in 5 of 8 yr for the 1980–87 period (Fig. 4). Predicted dates were poor and considerably earlier than those predicted in the remaining 3 yr. In two of those years (1981 and 1984) the discrepancy between the observed and predicted emigration dates was 9 d or 50% of the total variation in emigration timing seen in the 17-yr study. Nevertheless, all observations were within the 95% confidence interval for predictions (Fig. 4). We could identify no physical factors that could explain the discrepancy between observed and predicted emigration timing in the 3 yr poorly predicted or any that could increase the explained variance. Factors considered were the rate and direction of change of stream temperature (Jonsson and Rudd-Hansen 1985) and stream discharge during various periods preceding emigration, unusual meteorological events such as drought and storm frequency, and the lunar cycle (Grau 1981).

Dispersion of Emigration

An important component of emigration timing is the dispersion of emigration as measured by the inter-quartile range. In 12 of 16 yr 50% of chum salmon fry emigrated in 10 or fewer days (Fig. 5) and in only one year (1975) was the range greater than 14 d. In contrast, there was only one year (1985) in which 50% of the coho salmon smolts emigrated in less than 14 days, and in 8 of 17 yr the range was 21 d or greater (Fig. 5). For coho salmon fry the duration of emigration varied from 7 to 30 d. For all three groups, the range was statistically independent of the median date and numbers of emigrants, indicating that the range can be treated as a property of the life stage and is

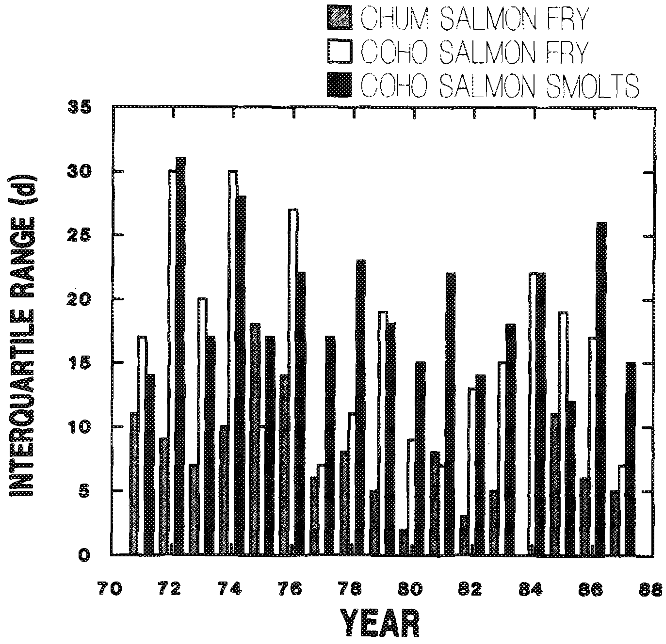

FIG. 5. Inter-quartile range of emigration time series for chum and coho salmon fry and coho salmon smolts by year.

not merely a statistical artifact of varying median emigration dates and emigrant numbers.

Comparison of Responses to Temperature Variation

Changes in the emigration timing of fry and smolts in response to temperature variation were remarkably different (Fig. 6). The responsiveness of the three groups to stream temperature change, as measured by the slopes of emigration timing–temperature relationships, differed significantly. Although the historical range of average stream temperatures for the spring (February 25 to median smolt emigration date) was similar to that for the egg incubation period, the variation in smolt emigration timing was considerably smaller than the variation in fry emigration timing. Over the historical temperature range of ≈3.6°C, emigration timing of coho salmon smolts varied 15 d, while emigration timing of fry varied 58 d for chum salmon and 73 d for coho salmon.

The temperature relationship for coho salmon smolts is close to one of temperature independence (Fig. 6). In contrast, coho salmon fry have a nearly constant thermal requirement for emergence over most of the historical range of stream temperature. Chum salmon fry are intermediate between the two life stages of coho salmon.

Discussion

Emigration timing for the coho and chum salmon fry was strongly temperature dependent, and for both species models derived in the laboratory that related temperature to maximum alevin wet weight provided excellent predictors of emigration timing for these wild populations. Our observations of emigration timing over 17 yr in a natural system fully supported Bams (1970) and Heming (1982) who speculated that MAWW could be used as a predictor of emergence and emigration readiness for Pacific salmon. Previous studies such as those of Rombough (1985), who observed a close correspondence between t_{MAWW} and ponding times in chinook salmon, and Mason (1976), who in a study of coho salmon emergence from artificial redds, observed that the heaviest alevins emerged at the time of peak emergence, were done in artificial conditions. The close agreement between these particular laboratory models and observations in the wild contrast with Crisp's (1988) general observation that laboratory models of emergence timing often failed to accurately predict emergence from natural gravels. Furthermore, the close agreement between t_{MAWW} predictions of emi-

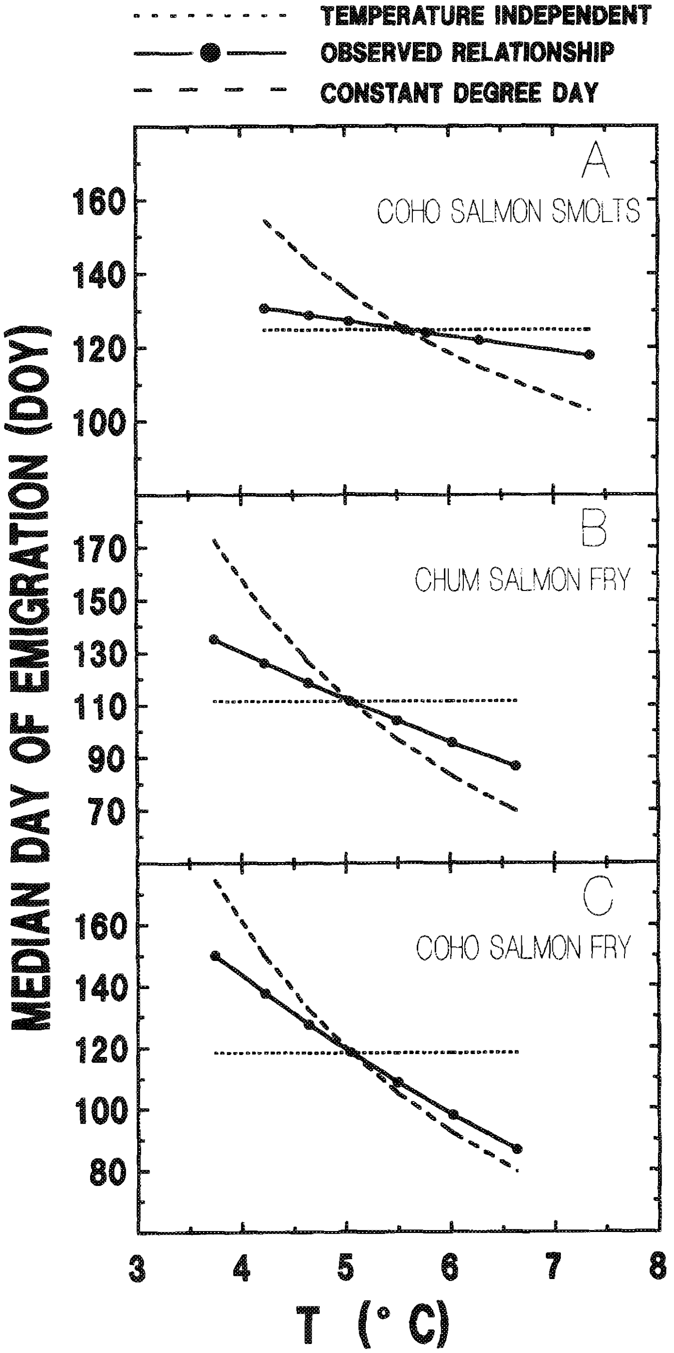

FIG. 6. Modeled and hypothetical relationships between median emigration date and temperature for (A) coho salmon smolts, (B) chum salmon fry, and (C) coho salmon fry. Hypothetical reltionships assume temperature independence (····) or constant thermal summation requirements (— — —). Temperature values indicated on the curves for the modeled relationships (—●—) are, from the left: historical minimum, 10%, 25%, median, 75%, 90%, and historical maximum. DOY = day of year.

TABLE 4. Characterizations of emigration time windows and associated patterns of emigration timing.

Window characterizations				Emigration timing	
Type	Width	Temporal shifts	Temporarl shift predictable	Temporal shifts	Dispersion
1	Narrow	Yes	Yes	Yes	Low
2	Narrow	Yes	No	No	High
3	Narrow	No	—	No	Low
4	Wide	Yes	Yes	Yes	Low/high
5	Wide	Yes	No	No	High
6	Wide	No	—	No	Low

gration timing and observed timing in Carnation Creek both before and after logging, support our contention that variability in emigration timing was being driven by variation in stream temperatures.

The timing and duration of emigration are determined by the timing and duration of spawning and by the interaction of developmental programs with local temperature conditions. The consistency of development rates over large geographic areas (Beacham and Murray 1987 exceptions are not unknown, e.g. Tallman 1986), suggests that adaptation to local conditions is mediated mostly by spawner behaviour rather than by variable development rates. Consequently, the time of spawning, probably on a scale of weeks, or even days, and spawning duration should be viewed as important adaptations to local conditions. Failure to recognize this has apparently compromised stock rebuilding programs in Oregon (Nickelson et al. 1986).

Lannan (1980) observed that the thermal requirements for emergence (and emigration) in an Oregon hatchery stock of chum salmon increased after one generation of hatchery operation. Hatchery fry emerged and emigrated before wild fry because water used in the hatchery was warmer than in the river. He speculated that decreased survival of the early emigrating fry led to selection of a hatchery stock with higher thermal requirements for emergence. Although there were no statistically significant indications of similar effects at Carnation Creek, there were some indications that such effects might have been present in the chum salmon. In all years during the period where effects of the logging perturbation were expected, fry emigrated later than predicted by the temperature model. Monitoring of the population is continuing.

The temperature model of coho salmon smolt emigration is entirely consistent with current understanding of the physiology of the smolt transformation. The most important stimulus for synchronization of the smolt transformation is probably the seasonal photoperiod cycle (Clarke et al. 1981; Wagner 1974). At Carnation Creek, the strongest correlations between temperature and smolt emigration were for averaging periods beginning on February 25, at which time the daylength (daylight plus civil twilight) is approximately 11.8 h. That value is in close agreement with laboratory experiments which have indicated a critical daylength threshold of between 11.5 and 12 h (W. C. Clarke, Pacific Biological Station, Nanaimo, B.C., pers. comm.). We conclude that the observed variability in the emigration timing of coho smolts was also being driven by temperature variation. Although there are undoubtedly many proximate factors which can effect quantifiable variability in emigration timing (Grau 1981; Solomon 1981), we suggest that such factors would tend to operate on a short time scale and would affect day-to-day rather than inter-annual variability.

The marked differences between the species and life-stages to temperature variation are important clues to the underlying selective pressures that constrain the timing of these important life history events. Brannon (1987) noted for sockeye salmon (*O. nerka*) that the slope of the emergence/emigration time-temperature relationship lies between zero indicating temperature independence and some negative value, (−0.11 for our study), indicating a constant thermal requirement for development. A slope of zero would enable a fish to emigrate on a fixed date, irrespective of temperature conditions in the stream. As the slope becomes more negative, the developmental process becomes increasingly responsive to temperature variability. Since the timing of emigration serves to synchronize fish movements with advantageous conditions in their rearing environments (Bams 1969; Northcote 1978; Walters et al. 1978; Brannon 1987), the ability to track temporal shifts in such time windows would be of adaptive value. We think that the differences in the temperature responses of the three groups in our study indicate differences in the characteristics of their respective time windows.

Such windows (Walters et al. 1978) may be characterized along three dimensions: the time open or width, the extent of temporal shifts, and the predictability of those temporal shifts from environmental conditions in streams (Table 4). Although the dimensions are probably continuous we have assumed them dichotomous. Each window type is associated with a characteristic pattern of emigration. The width of the time window cannot be deduced from the emigration pattern alone, but can be inferred from observations of the timing and magnitude of mortality during emigration. Only window type 4 (Table 4), a wide window with predictable temporal shifts might have a range of emigration patterns associated with it. Emigration dispersions with this window type should tend to be low rather than high, either because being first through a wide predictable window is potentially advantageous or because the predictability of the window allows highly synchronous emigration as a predation-minimizing strategy.

The relative temperature insensitivity of coho smolt emigration timing and their protracted emigration period suggest either a type 2 or type 5 window (Table 4). The work of Bilton et al. (1982) and Thedinga and Koski (1984), suggests that changes in emigration timing of 1 wk can reduce survival by as much as 50%, implying a narrow (type 2) rather than wide window (type 5). The temperature sensitivity and narrow dispersion of chum salmon fry emigration suggests either a type 1 or type 4 window (Table 4). Simulation studies (Walters et al. 1978) and estuarine studies (Healey 1979; Sibert 1979; Bax 1983; Murphy et al. 1988) suggest that the window open to chum salmon fry is perhaps as wide as 6 wk, consistent with a type 4 window. The much tighter synchrony of chum salmon emigration compared with coho salmon smolt emigration suggests that the former species, emigrating within a broad window, can avail itself of the benefits of predator saturation. That strategy is closed to coho salmon smolts who are dealing with an unpredictable and narrow window. Alternatively, the synchrony of chum salmon emergence could have no adaptive value, but instead be simply the outcome of the behaviour of their parents, whose synchronous spawning might itself be an adaptive response to minimize bear predation on the spawning grounds. However, in streams where there are distinct early (October) and late (January) spawning stocks, synchronous fry emigration involving both stocks is observed (Koski 1975; Tallman 1986), suggesting that synchronous emigration is adaptive rather than merely fortuitous.

The large temporal shifts and wide dispersion of coho salmon fry emigration are associated only with a type 4 window (Table 4). Coho salmon fry show a constant degree day requirement at all but the oldest expected temperatures. There is convincing evidence that early emergence is associated with higher fry-to-smolt survival (Holtby 1988), which should favour low, rather than high, dispersion in emergence timing. However, early emergence might also have risks, principally the increased chance of encountering late winter storms (Hartman et al. 1984; Nickelson et al. 1986). Those risks might outweigh the benefits of synchronous emergence and favour the high dispersion emergence pattern that is observed.

An important parameter of the windows, as we characterize them, is their predictability, but it is not immediately obvious how ocean conditions at the time of emigration can be anticipated from stream temperatures before emigration. Winter stream temperatures in Carnation Creek are strongly correlated with sea surface temperatues around the time that the coho salmon smolts and chum salmon fry enter the ocean ($r = 0.75$, $p < 0.001$, $n = 52$). Stream temperatures over the winter are also significantly correlated with sea surface salinities in the spring ($r = -0.20$, $p < 0.05$, $n = 52$). Sea surface temperatures and salinities are correlated with early marine survival of chum salmon fry (Holtby and Scrivener 1989) and coho salmon smolts (Holtby 1988; Holtby and Scrivener 1989; Nickelson 1986). It is conceivable therefore, that stream temperatures could be used by the fish to synchronize their ocean entry with favorable conditions.

The differences between the three groups in the extent to which they track stream temperatures seems to agree with what is known about their life histories on entering the stream or ocean. Coho salmon fry remain in the stream after emergence and we assume that temperature conditions in the stream during the winter and spring are good predictors of stream conditions in the spring. Hence coho salmon emergence tracks stream temperature tightly, especially at higher temperatures. Buffering is present at cold temperatures. Presumably it is better to emerge under less than ideal conditions in late May than to delay emergence until mid-summer. Chum salmon fry probably time ocean entry to correspond with vernal peaks of productivity (Walters et al. 1978). To the extent that ocean production is dependent on temperatures, ocean productivity can be predicted from stream temperatures. However, since freshwater conditions are likely more variable than those in the ocean, the dependence of emigration timing on temperature is more strongly buffered against temperature change in chum salmon than it is in coho salmon. Variation in coho salmon mortality is probably dependent on variations in predation intensity (Fisher and Pearcy 1988; L. B. Holtby, unpubl. data) and not on variations in ocean production. The extent to which variations in predator abundance and appetite are predictable from stream temperatures is unknown, but judging by the near constancy of emigration timing and the wide dispersion of emigration, no predictor is available to the fish in the stream.

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