

Temperature and Flow Effects on Migration Timing of Chinook Salmon Smolts

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Abstract.—Physiological and behavioral changes occur in the spring when juvenile Pacific salmon *Oncorhynchus* spp. undergo smolting. Survival is maximized if the timing of these changes coincides with migration from fresh to marine environments. Therefore, understanding how environmental conditions influence the onset, duration, and termination of smolting can have substantial management implications, particularly for flow-controlled rivers. We used an information-theoretic model comparison analysis to investigate the roles of daily mean temperature, temperature experience (accumulated thermal units [ATU]), photoperiod, and flow on the timing of the downstream migration of Chinook salmon *O. tshawytscha* smolts from the Nechako River in central British Columbia. Both binary (migration or not) and count (the total number of migrants) models were developed that predicted the downstream migration of Chinook salmon based on data collected from fish captured at rotary-screw traps from 1992 to 2004. The analyses identified a combination of temperature experience, flow, and the number of spawners as best able to describe the observed migration patterns. In addition, increasing ATU had a positive influence on migration, while increasing flow had a negative influence. Temperature experience was found to have more influence on migration than daily mean temperature. The predictive ability of each model was tested with 2 years of independent data. The count model accurately predicted the general trends in migration and, in particular, the termination of migration, but not the daily fluctuations in movement. By contrast, the binary model predicted whether fish would migrate on a given day with accuracies of 93% and 99%, respectively, for the 2 years tested. Temperature experience was more strongly linked to migration than the daily or threshold temperature; warmer temperatures resulted in earlier migration. Our data suggest that flow plays an important role once migration is under way and may even serve as a termination cue. Furthermore, the number of migrants and the probability of migration was positively related to the number of spawners. Based on the results of this study, flow manipulations that change the timing, duration, or magnitude of temperature and flow in the spring could affect the migration of Chinook salmon. Both temperature and river flow should be considered when one is managing flow-controlled watersheds for salmon productivity.

Environmental variables play an important role in smolting—the development of saltwater tolerance in juvenile salmon. It is generally thought that environmental priming factors (photoperiod and temperature) cue physiological changes related to increased saltwater tolerance, and environmental releasing factors (temperature, flow, and turbidity) trigger actual migration (McCormick et al. 1998). While increased photoperiod is important for the physiological changes necessary for seawater residency, other synchronous environmental changes such as warming water temperatures, increased flow, and increased turbidity are necessary to ensure that fish arrive at the marine environment at the appropriate time. Poor synchrony between smolting and entrance into the marine

environment can reduce the probability of survival of individual fish (Zaugg et al. 1985). Despite the importance of the smolting process and the interactions with migration, little information exists on factors that control the timing of migration. Photoperiod, temperature, flow, species, adult escapement, rearing history, and size of juveniles have all been linked to salmonid migration to some extent (Roper and Scarnecchia 1999). In addition, differences in migration distances among populations of the same species can further compound the problem of understanding migration cues within a species.

Early theories on the migration of smolts suggested that juvenile fish were displaced downstream due to limited swimming ability coupled with increased spring flow (Thorpe and Morgan 1978). More recent experiments testing the swimming performance of salmon smolts suggest that it is unlikely that downstream movement is involuntary (Peake and McKinley 1998). Increasing flows in the spring, however, may serve to stimulate migration in specific populations of Atlantic salmon *Salmo salar*; increasing temperature is

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also a potential controlling factor (Hvidsen et al. 1995; McCormick et al. 1998). In addition, photoperiod, which has a significant effect on the physiological changes associated with smolting, may also play a role in determining the onset of migration. Given the number of environmental factors that are changing in the spring when migration occurs, it is difficult to determine what role a particular variable or combination of variables has on the process. Similarly, it is unknown what effect there will be if certain environmental cues are delayed, accelerated, or are asynchronous. These issues are particularly relevant in flow-controlled systems where manipulations of the hydrograph can result in substantial changes to the flow regime and temperature of the system. From a management perspective, it is crucial to understand what effect, if any, the establishment of particular flow regimes and alterations in rate of temperature change can have on the smolting process.

The objective of this study was to investigate the relationship between smolt migration and changes in environmental variables by correlating 13 years of Chinook salmon *Oncorhynchus tshawytscha* smolt migration data with changes in five variables: water temperature ($^{\circ}\text{C}$), accumulated thermal units (ATU), discharge (m^3/s), numbers of spawners, and photoperiod (hours of daylight). The data were collected between 1992 and 2004 from the Nechako River, located in central British Columbia. The river's flow has been controlled since 1952 following the construction of Kenny Dam. We used the fish count data to develop ecologically plausible sets of explanatory binary and count models. The binary analysis (presence-absence data, logistic regression) model focused on whether migration occurred on a given day. The count analysis (number of migrants, negative binomial regression) model focused on the numbers of fish migrating on a given day. We then used these models and an Information Theoretic Model Comparison (ITMC) procedure to evaluate competing hypotheses explaining the timing of migration. This analysis provided a better understanding of factors that influence smolt migration in a flow-regulated river and specifically how yearly differences in flow and temperature affected migration patterns.

Methods

Data collection.—The data used in the generation of the predictive Chinook salmon migration models were collected from 1992 to 2004 as part of the juvenile out-migration study by the Nechako Fisheries Conservation Program (NFCP). Three rotary-screw traps (RST) were fished in the Nechako River at Diamond Island, located 81 river kilometers (rkm) downstream from the Kenny

Dam (Figure 1). Chinook salmon smolts migrating in the Nechako River are all progeny of wild spawners as there has been no hatchery production of smolts in the system. Spawning sites exist upstream from the trapping site with the primary site being located in the vicinity of rkm 16. Tributaries upstream from the trapping site are small and do not provide Chinook salmon spawning habitat. Flow regulation in the system involves releasing water from the Nechako Reservoir into the Cheslatta River system, which joins the Nechako River at the Cheslatta Falls located at rkm 9. The falls represent the upstream limit of Chinook salmon distribution in the system as the Kenney Dam releases no water into the dewatered Nechako Canyon. Temperatures in the Nechako River downstream from the Cheslatta Falls typically range from 0°C to 3°C from January to March with peaks in the range of $15\text{--}20^{\circ}\text{C}$ achieved by July. Discharge in the system is typically maintained from 30 to $35 \text{ m}^3/\text{s}$ from September to March and increases to approximately $60 \text{ m}^3/\text{s}$ by July. In mid-July, flow is increased to approximately $285 \text{ m}^3/\text{s}$ to reduce river temperatures to facilitate upstream migration of adult sockeye salmon *O. nerka* in August.

Installation and removal dates of the traps varied from year to year depending on river conditions. In general, traps were fished from the beginning of April through the end of July. Traps were established at the same location (one shore trap and two mid-channel traps) each year. Traps were checked twice daily at 0800 and 1900 hours. Data from 1993 to 2003 ($n = 1,125$ trap checks) were used in the construction of the model while data from 1992 and 2004 ($n = 217$ trap checks) were kept separate for use in model validation. Average daily Chinook salmon captures for 1992–2004 along with average flow and temperature for the same period are shown in Figure 2. Between 1989 and 1998, the average fork length of Chinook salmon smolts captured at the Diamond Island trapping site ranged from 95 to 105 mm while age-0+ fish were less than 50 mm (NFCP 2005). Measurements of gill Na^+, K^+ -ATPase activities for migrants in 2004 were significantly greater than values for parr confirming that the fish were smolts (Sykes 2007).

Model development.—We used logistic regression to construct binary models to explain the daily presence (1) or absence (0) of migrating Chinook salmon. We used count models to explain the variation in the number of migrating Chinook salmon captured on a given day. Count models were premised on a negative binomial (negative binomial regression models [NBRMs]) or Poisson distribution (Poisson regression models [PRM]). The likelihood-ratio test allowed us to detect overdispersion and determine whether the

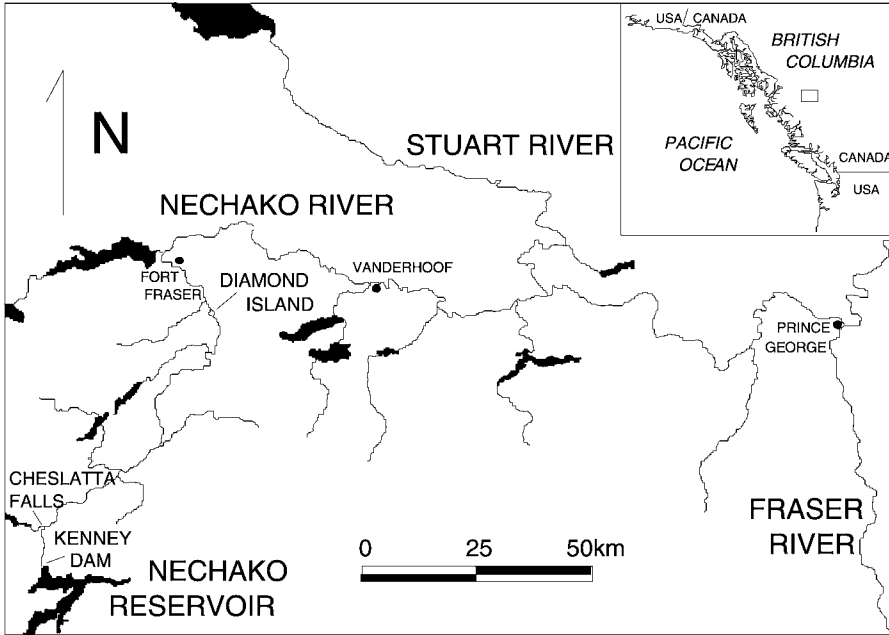


FIGURE 1.—Location of the rotary-screw traps at Diamond Island in the Nechako River system. Water Survey of Canada data were collected at Cheslatta Falls.

NBRM or PRM was more appropriate. Both distributions tend to underpredict the occurrence of zero counts relative to the observed data for datasets with a large number of zero counts (Lord et al. 2005; Long and Freese 2006) requiring a zero-inflated version (ZINB or

ZIP). In addition to predicting the zero counts that occur during the migration period, these models take into account situations where migration will never occur (for example, due to time of year) and include that component to help account for the excess zeros in

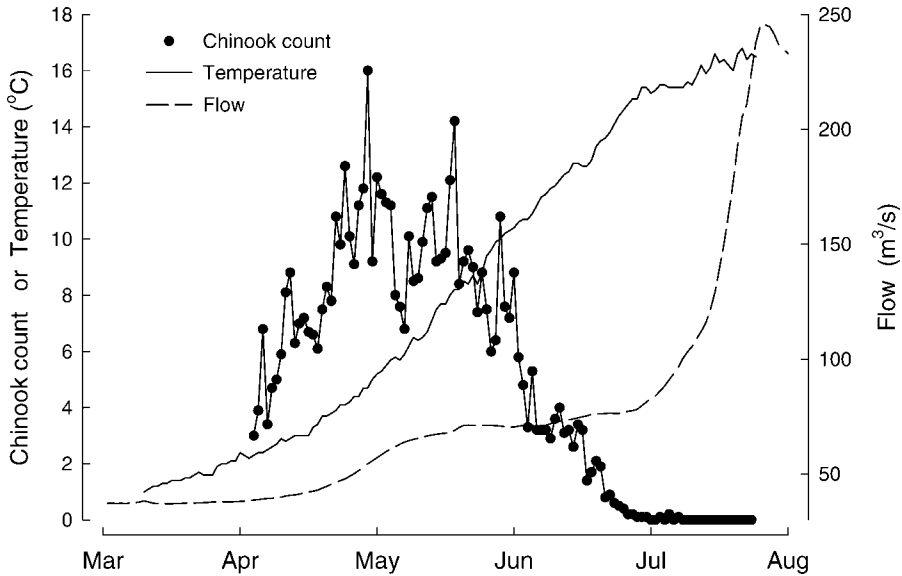


FIGURE 2.—Average daily Chinook salmon captures, average flow, and average temperature in the upper Nechako River for the period 1992–2004.

the dataset. We used a Vuong test to compare the output of a NBRM to that of a ZINB and determine whether a zero-inflated model was necessary (Vuong 1989). All statistics were completed using Stata version 9.2 (Statacorp, College Station, Texas).

Model parameters.—We developed candidate models from a small set of predictor variables recognized as important for explaining the timing of migration of juvenile Chinook salmon: temperature (°C), accumulated thermal units (ATU, sum of daily mean temperatures [°C]), flow (m³/s), and photoperiod (hours of daylight per day). In addition to combinations of these variables, all binary and count models included a term representing the number of spawners, a factor that can influence year-to-year variation in migration numbers and also the probability of migration. The brood year for migrating Chinook salmon in the Nechako River is 2 years before the date of migration. Additionally, a quadratic equation was used to describe variables that have a nonlinear distribution during the migration period such as temperature and ATU. All parameters with the exception of that for spawners were tested to see whether use of a quadratic equation was appropriate; however, only temperature² and ATU² resulted in a lower small-sample-bias-corrected Akaike's information criterion (AIC_c) score than in the same model with only the linear parameter.

Both mean daily water temperature data and flow data were collected from the Water Survey of Canada (WSC) station located upstream from the trap site near Cheslatta Falls (Station 08JA017). Although this station is located approximately 70 rkm upstream from the trap site, it is the most reliable and continuous dataset available for the upper Nechako River and provided a record of river temperatures before trap installation, which was important for calculating ATUs. The gauge data are considered representative of conditions at the trap site due to the lack of large tributaries between the two sites and the fact that the gauge is upstream from the traps. Comparison of data collected at the trap site and at the WSC station for days when both were available did not show a significant difference in mean daily temperature ($P = 0.1$) or flow ($P = 0.08$). Accumulated thermal units were calculated beginning on March 9, the date on average (1987–2004) where mean daily water temperature first reached 1°C for the year. Photoperiod data were calculated for the latitude and longitude of the nearest residential community to the trapping site (Fort Fraser, British Columbia; 54°04'N, 124°33'W). The number of spawners was determined by aerial surveys completed by Fisheries and Oceans Canada during the spawning period each year.

Models.—We developed 11 models (Table 1) to represent biologically plausible hypotheses to explain juvenile Chinook salmon migration. During the model development stage, the collinearity of the variables was assessed because in situations where two or more variables have a strong collinear relationship, an infinite number of regression coefficients can be generated that will work equally well in the model produced (Menard 2001). We used a linear regression to calculate tolerance statistics for each of the parameters in the model. A tolerance statistic is equivalent to $1 - R^2$ and values less than 0.1 suggest strong collinearity (Menard 2001). An initial assessment of collinearity identified a linear relationship between ATU² and temperature² (tolerance value of 0.20 and 0.12, respectively). As a result, no models were tested that included both of those variables. The tolerance scores for the remaining combinations of variables exceeded 0.3 and, therefore, collinearity was not considered a problem.

Model selection.—Applying the ITMC technique, we used AIC to identify the most parsimonious model. The AIC_c form, which is corrected for small-sample bias, was used in place of the standard AIC value as AIC_c has been shown to converge to the standard AIC value as the sample size increases (Burnham and Anderson 2004). The formula for calculating AIC_c is as follows:

$$AIC_c = -2LL + 2K + 2K \cdot (K + 1) / (n - K - 1),$$

where LL is the log likelihood, K is the number of parameters, and n is the sample size. The term Δ_i represented the difference in AIC_c between the most parsimonious model and all subsequent models. If Δ_i is less than 2, models are too similar to be ranked and the model with the fewest parameters can be selected (Anderson et al. 2000). Also, we report the AIC weight (AIC_w) for each model. This value represents the probability that the corresponding model is the best model of the set of tested models. For each parameter, we summed the AIC_w values from all models that contained that parameter; this sum measures the relative importance of each parameter across the model set. For the best binary and count models, a β coefficient was generated for each parameter, the sign of which corresponded to the direction of the effect. We used the Z -statistic to assess the statistical significance of the individual parameters. Significance was determined as $P < 0.05$.

Predictive ability.—As recommended by Guthery et al. (2005), we used migration data withheld from model construction (years = 1992 and 2004) to conduct an independent validation of the most parsimonious models. For the binary analysis, the following binary

TABLE 1.—Model selection statistics for the candidate binary and ZINB count models to predict the downstream migration of juvenile Nechako River Chinook salmon. For models with a quadratic term, the linear component of the parameter was also included; ATU = accumulated thermal units.

Model	Rank	AIC _c	ΔAIC _c	AIC _w
Binary				
ATU ² + flow + photoperiod + spawners	1	574.212	0.0	0.580
ATU ² + flow + spawners	2	574.856	0.6	0.420
ATU ² + spawners	3	613.724	39.5	0.000
ATU ² + photoperiod + spawners	4	615.563	41.4	0.000
Temperature ² + flow + spawners	5	691.057	116.8	0.000
Temperature ² + flow + photoperiod + spawners	6	692.963	118.8	0.000
Temperature ² + photoperiod + spawners	7	753.737	179.5	0.000
Temperature ² + spawners	8	753.786	179.6	0.000
Flow + photoperiod + spawners	9	1,092.775	518.6	0.000
Photoperiod + spawners	10	1,127.137	552.9	0.000
Flow + spawners	11	1,373.704	799.5	0.000
ZINB				
ATU ² + flow + spawners	1	4,736.510	0.0	0.637
ATU ² + flow + photoperiod + spawners	2	4,737.637	1.1	0.363
Temperature ² + flow + spawners	3	4,784.116	47.6	0.000
Temperature ² + flow + photoperiod + spawners	4	4,785.487	49.0	0.000
ATU ² + photoperiod + spawners	5	4,810.104	73.6	0.000
ATU ² + spawners	6	4,810.571	74.1	0.000
Temperature ² + photoperiod + spawners	7	4,850.677	114.2	0.000
Flow + spawners	8	4,852.214	115.7	0.000
Temperature ² + spawners	9	4,852.479	116.0	0.000
Flow + photoperiod + spawners	10	4,854.113	117.6	0.000
Photoperiod + spawners	11	4,896.938	160.4	0.000

logit model was used to generate the predicted probability of Chinook salmon migration:

$$Y = \frac{\exp(\beta_0 + \beta_1x_1 + \beta_2x_2 + \dots + \beta_ix_i)}{1 + \exp(\beta_0 + \beta_1x_1 + \beta_2x_2 + \dots + \beta_ix_i)},$$

where β₀ is the intercept term, β_i is the coefficient for each covariate in the model, and x_i is the value of the covariate. Pearson’s standardized residuals were used to assess the difference between the observed and predicted values. Standardized residuals have a normal distribution and therefore should have a mean of 0 and a standard deviation (SD) of 1. In addition, 95% of the residuals should fall between -2 and 2 with larger and smaller values identifying cases where the model works poorly or that exert more than their share of influence on the model parameters (Menard 2001).

We used the receiver operating characteristic (ROC) curve and withheld data to evaluate the proportion of correctly and incorrectly classified migration events (Pearce and Ferrier 2000). The general guidelines for interpreting the area under the ROC curve with respect to predictive ability are: poor (0.5–0.7), reasonable (0.7–0.9), and very good (0.9–1.0) (Swets 1988). For the count analysis, we used the Stata program prcounts.ado (Long and Freese 2006) to predict the number of migrating salmon. Due to nonnormality of the data, a nonparametric Wilcoxon rank-sum test was used to compare observed and predicted counts for 1992 and 2004.

Results

The negative binomial regression model (NBRM) was preferable to the Poisson regression model (PRM) because of overdispersed count data ($G^2 = 3180.01$, $P < 0.001$). In addition, when the NBRM and the ZINB were compared, the large number of zero counts resulted in a better fit for the ZINB (Vuong test = 0.98, $P = 0.16$). Although not significant, the result was confirmed by lower AIC_c scores and better predictive ability of the ZINB compared with the same model calculated using the NBRM.

Based on AIC_c scores, a combination of ATU², flow, photoperiod, and spawners best modeled the probability of Chinook salmon migration (binary analysis; Table 1). Models that included spawners as a variable consistently had lower AIC_c scores than the comparable model without spawners included. Whether spawners was included or not, however, did not change the rank of the models. Consequently, spawners was included in all binary models. The second-ranked binary model (ATU² + flow + spawners) had an AIC_c score only 0.6 points greater than the model ranked first and, because of the marginal difference in AIC_c scores, we determined the best model to be the one with the fewest variables. For the count analysis, the same two models were ranked first and second based on AIC_c score except that the model ranked first (ATU² + flow + spawners) was also the simplest and therefore was selected (Table 1). The combined AIC_w of each of

TABLE 2.—Regression outputs for binary and count models to predict the downstream migration of juvenile Nechako River Chinook salmon; ATU = accumulated thermal units.

Variable	β	SE	Z	P	95% confidence limits	
					Lower	Upper
Binary model						
ATU	0.0126	0.0025	4.97	<0.001	0.0077	0.01762
ATU ²	-2×10^{-5}	3.6×10^{-6}	-7.80	<0.001	-3.51×10^{-5}	-2.10×10^{-5}
Flow	-0.0142	0.0026	-5.93	<0.001	-0.1925	-0.0092
Spawners	0.0007	0.0002	4.57	<0.001	0.0004	0.0010
Constant	1.489	0.4186	3.56	<0.001	0.6682	2.3092
Count model						
ATU	0.0083	0.001	8.08	<0.001	0.0063	0.0103
ATU ²	-1.7×10^{-5}	1.8×10^{-6}	-9.31	<0.001	-2.1×10^{-5}	-1.4×10^{-6}
Flow	-0.0119	0.0014	-8.60	<0.001	-0.0147	-0.0092
Spawners	0.0003	3.9×10^{-5}	9.81	<0.001	0.0003	0.0005
Constant	1.3985	0.1457	9.60	<0.001	1.1129	1.6841
Count model (inflate portion)						
ATU	0.0178	0.0032	5.59	<0.001	0.0119	0.0241
Constant	-11.1827	1.8484	-6.05	<0.001	-14.8056	-7.5599

the variables showed ATU² and flow had a score of 1.0, which was higher than any of the other variables with the exception of that for spawners, which had been included in all other models.

Beyond the models ranked first and second, the rankings of the remaining models differ for the two distributions. In the case of the binary model, the variable ATU² was found in each of the top four models, with temperature² found in the following four (ranked 5–8). In the case of the count model, the variable flow was included in each of the top four models and similar to the binary models, ATU² was found to result in lower AIC_c scores than the corresponding temperature² model.

Model Coefficients

The coefficients generated for each of the variables included in the most parsimonious binary and count models (Table 2) had a statistically significant affect on migration ($P < 0.001$). Pearson's standardized residuals for the binary analysis indicated that no records influenced the model disproportionately (mean = 0.002, SD = 0.97; 96% of the values being between -2 and +2). For both the binary and count models, flow and the squared component of the ATU quadratic were found to have a negative influence on migration, while the linear component of the ATU quadratic, and spawners had a positive influence.

We also considered the combined effects of flow and ATU, as changes in these variables do not generally occur independently. Results of the modeling analysis suggest that both high flow and warmer temperatures are correlated with a decline in migration. Therefore, years with high ATU and high flow would be expected

to have a shorter migration period than those with low ATU and flow. To determine whether this was the case for the Nechako River, each of the 13 years included in the dataset were ranked based on ATU (March 9–July 31) and flow (cumulative discharge, March 1–July 31). The number of days it took to capture 50% of the total yearly catch was then compared for the 3 years with both high ATU and flow to the 3 years with both low ATU and flow. In cooler low-flow years it took 8 d longer to reach the median catch than it did in warmer high-flow years (40 versus 32 d, respectively). Similarly, on average, the date of peak migration (defined as date where the greatest number of fish were captured) was approximately 12 d earlier in the high ATU–flow years (May 6 versus May 18), while the date of migration termination (defined as last date smolts were captured) was 13 d earlier (June 7 versus June 20). Although the majority of trapping data were collected after April 1, there was one high ATU–flow year (1992) where conditions allowed for installation of the traps on March 15. A total of 20 migrating age-1+ Chinook salmon were captured from March 15 to 30, which represents 9% of the total number of fish captured for the remainder of the sampling period (April–July, $n = 225$).

Model Validation

For both 1992 and 2004, independent migration data were an excellent fit to the best binary model (Figure 3). The ROC analysis had an area under the curve of 0.93 and 0.99 for 1992 and 2004, respectively. For both years, the model accurately predicted the transition from continuous migration in early spring to no migration by mid-June. Results of the model

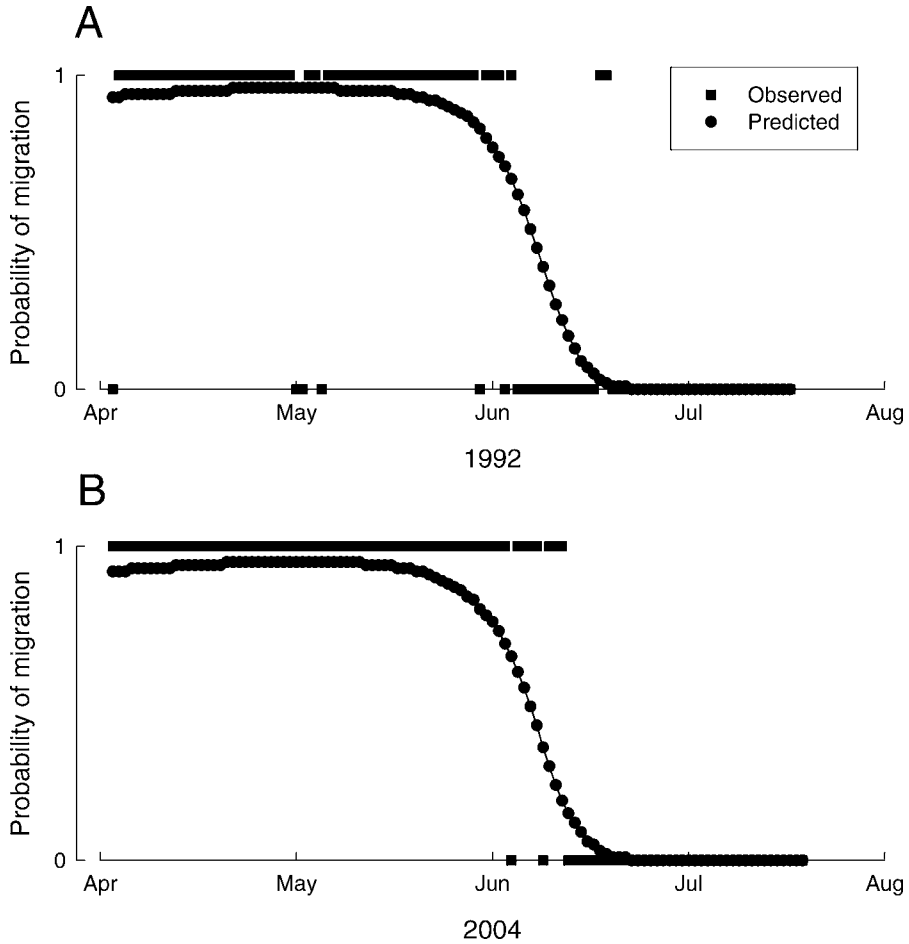


FIGURE 3.—Observed and predicted probabilities of downstream juvenile Chinook salmon migration from the Nechako River for (A) 1992 and (B) 2004. The observed data are from rotary-screw trap (RST) captures between April 4 and July 20. The predictions are based on a logistic regression model generated from RST capture data in combination with accumulated temperature unit and flow data for the Nechako River from 1993 to 2003.

validation for the count model (Figure 4) show that for 1992 the model tended to overpredict the migration numbers, while for 2004, the model results were more representative of mean migrant numbers. For both years, the model was not able to recreate the daily fluctuations in migrant numbers, but was successful at identifying the end of the migration period.

The Wilcoxon rank-sum test revealed a significant difference between predicted and observed counts of migrating salmon for 1992 ($Z = -4.55, P < 0.001$), but not for 2004 ($Z = -1.03, P = 0.30$). An analysis of the residuals for 1992 and 2004 indicated an average overprediction of 3.3 and 0.3 fish, respectively. During both years, the observed and predicted counts began to converge towards the middle of June. Applying a paired-sample t -test we found no statistical differences

in the proportion of each count observed and predicted for either 1992 ($t = 0.12, P = 0.91$) or 2004 ($t = 0.08, P = 0.98$). The total predicted and observed yearly Chinook salmon counts for 1992–2004 (Figure 5) showed that before 1998, the model overpredicted the number of Chinook salmon in 5 of 6 years by an average of 203 fish. Alternatively, from 1998 and 2004, there was an average underprediction of 80 fish despite the model overpredicting counts in 4 of 7 years. This was primarily due to an underprediction of 778 fish in 1998.

The number of juvenile Chinook salmon captured from 1992 to 1997 was significantly lower than for 1998–2004 (two-sample t -test: $t = -8.61, P < 0.001$) (Figure 5). Flow and temperature data for the same periods showed that both average flow and ATU were

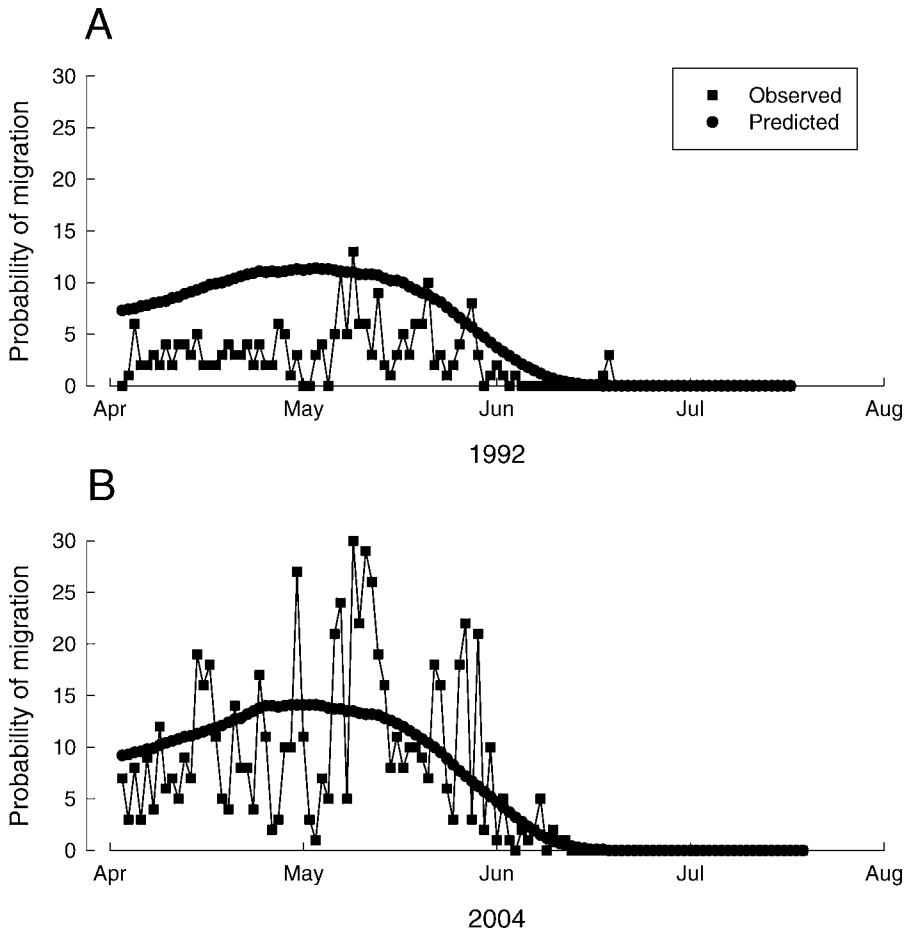


FIGURE 4.—Observed and predicted counts of juvenile Chinook salmon in the Nechako River for (A) 1992 and (B) 2004. The observed counts are from rotary-screw trap (RST) captures from April 4 to July 20. The predictions are based on a ZINB model (see text) generated from RST capture data in combination with accumulated temperature unit, flow, and spawner data for the Nechako River from 1993 to 2003.

significantly higher (two-sample t -test: $t = 11.6$ and -10.1 , respectively; $P < 0.001$) for the period from 1992 to 1997 than for the period from 1998 to 2004. Early migration before trap installation may have played a role in this difference, but it does not realistically explain the 5–6 fold increase in smolt numbers observed in cooler lower-flow years (1998–2004). Other factors probably influenced the observed variation in migrants. For example, there was a significant increase in spawner numbers for 1998–2004 (two-sample t -test: $t = -2.48$, $P = 0.04$). Additionally, during high-flow years there was a greater possibility of migrating fish bypassing traps as each RST would sample a smaller portion of the river, resulting in fewer captured fish. Although this suggests that the rotary-screw sampling method may

have led to inaccuracies in the number of Chinook salmon counted, the count and binary models produced similar explanatory variables. Results of the binary models were not influenced by inaccurate or imprecise count data.

Discussion

This study demonstrates an application of the ITMC approach to fisheries research using two of the most common forms of ecological data: presence–absence (binary) and count. The binary model addressed whether downstream migration of Chinook salmon smolts occurred on a given day. Results revealed general factors influencing smolt migration from the system and provided a means of assessing how manipulations of river conditions might affect the

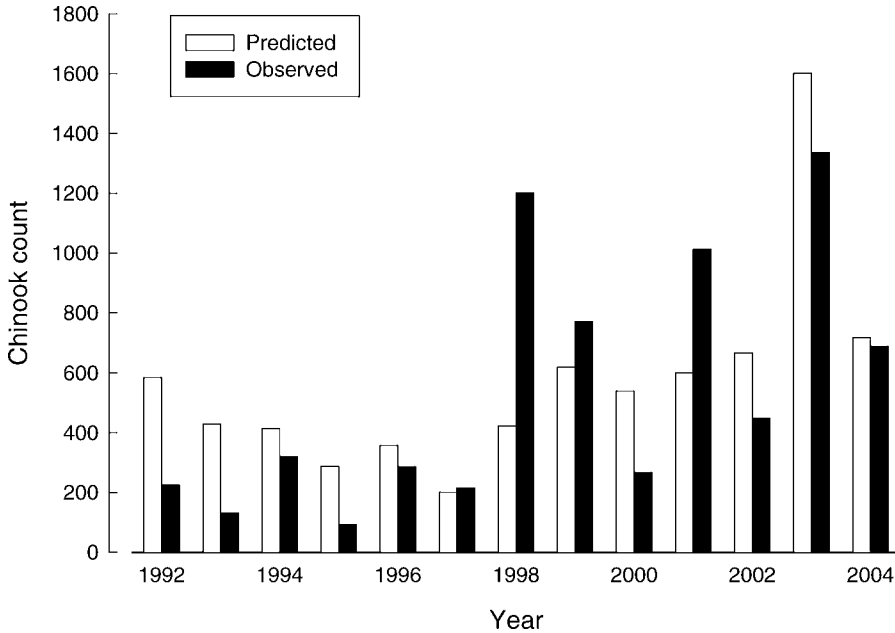


FIGURE 5.—Total predicted and observed Chinook salmon smolt counts for the Nechako River for 1992–2004. The observed data are based on rotary-screw trap (RST) captures. The predictions are based on a ZINB model generated from RST capture data along with accumulated temperature unit, flow, and spawner data from the Nechako River for 1993–2003.

probability of fish migration. For the second analysis, the count model used the numbers of fish captured from an established sampling program to assess how temperature, flow, and photoperiod affect the numbers of fish migrating. Although the models developed in this study are specific to the Nechako River population of Chinook salmon, similar techniques could be applied to other systems to develop population-specific models. In addition, the general conclusions from this analysis may have direct applicability to other flow-controlled rivers that support populations of Chinook salmon or other salmon species.

Migration Controls

Models were developed in our study to examine environmental factors that influence timing of migration for Chinook salmon smolts. Previous work has shown that the physiological changes associated with smolting strongly depend on seasonal changes in the environment (see Hoar 1987 for a review). Juvenile Chinook salmon captured in the Nechako River during the spring were smolts; measurements of gill Na^+, K^+ -ATPase activities for migrants in 2004 were significantly greater than values for parr (Sykes 2007). The loss of smolt characteristics is also controlled by environmental factors, particularly temperature (McCormick et al. 1997). Our results, therefore, provide information on the timing of migration in relation to

environmental factors. Although, it is possible that the decrease in migrants observed in our study is related to the depletion of the potential pool of migrants, timing of when Chinook salmon leave the Nechako River was the issue addressed in our study.

The results of both analyses show that a combination of temperature experience (ATU) and flow explain the observed migration data better than any of the variables individually. Although photoperiod was not included in the simplest binary model ($\text{ATU}^2 + \text{flow} + \text{spawners}$), it was included in the model that had the lowest AIC_c score. McCormick et al. (1998) also reported that a combination of environmental factors, rather than a single factor, was involved in the downstream migration of Atlantic salmon. They further differentiated priming factors (e.g., photoperiod and temperature), which initiate the physiological changes associated with smolting, and releasing factors (e.g., temperature, flow, and turbidity), which trigger the migration. Our study focused on the role of environmental variables during the migration period, and although it is difficult to assign a specific role to each of the variables involved, knowing that a combination of factors must be considered provides direction for future studies. Furthermore, our results suggest that managers should consider how manipulations will affect multiple potentially interacting variables as opposed to a single independent environmental factor.

Another important result was that both model analyses showed that temperature experience (ATU) explained migration timing better than daily mean temperature (Table 1) since models with ATU consistently had lower AIC_c scores than did the same model with temperature. This finding agrees with Zydlewski et al. (2005), who found that in a controlled experiment, temperature experience was more relevant to both the initiation and termination of downstream movement of Atlantic salmon compared with a temperature threshold. Other studies found a direct relationship between gill Na^+,K^+ -ATPase activity and salinity tolerance and temperature experience during migration and showed that anadromous fish that experience warmer rearing conditions will have an earlier peak in gill Na^+,K^+ -ATPase activity (McCormick et al. 1997, 1999; Handeland et al. 2004). Accumulated thermal units also has been linked to the loss of smolt characteristics and, in particular, the decline in gill Na^+,K^+ -ATPase activity (McCormick et al. 1997; 1999).

Without an increase in photoperiod, smolting will not occur and the importance of photoperiod to the smolting process cannot be disputed. The majority of work on photoperiod has focused on the importance of this factor for initiating physiological changes as opposed to modifying behavior associated with migration (e.g., McCormick et al. 1987; Saunders et al. 1989). The results of our study, however, suggest that once smolting has been initiated, photoperiod may not affect characteristics of migration such as peak and termination in movement. Although photoperiod was included in the top-ranked binary model and second-ranked count model, models developed with only the photoperiod variable were ranked either lowest (count) or second lowest (binary) (Table 1). Additionally, the top-ranked binary model without photoperiod predicted migration pattern for 2 years of independent data (1992 and 2004) with an accuracy of 93% and 99%, respectively. The limited role of photoperiod as identified by both of the analyses should not be viewed as a contradiction of previous work. Instead, the results should be viewed in the context of the goals of the study, which were to assess the role of environmental variables that control smolt migration once the physiological changes associated with smolting had begun.

Flow

The values of coefficients generated for both binary and count models indicated that flow had a negative influence on the probability of migration. The negative value of the flow coefficient was unexpected given that previous studies have found that increasing flow

facilitates downstream migration (e.g., Connor et al. 2003). Such results suggest that flow augmentation during the migration period could increase the survival of migrating salmonids (Connor et al. 2003; Smith et al. 2003). In particular, Raymond (1979) showed that a decrease in flow in the Columbia River delayed migration of spring Chinook salmon and steelhead *O. mykiss* smolts. A review of the hydrograph before the 1952 installation of the Kenny Dam (see French and Chambers 1997) showed that historically the spring peak freshet flows occurred in the middle of May. However, the migration of Chinook salmon smolts from the Nechako River (Figure 2) began before the historic freshet, suggesting that flow is not involved in the onset of migration. While migration numbers initially increase as flow increases, the peak in migration numbers tends to occur before the peak in flows and there is actually a decrease in migrant numbers during the period of highest flows. In particular, the substantial increase in flow that occurs in July, as part of the flow management strategy to lower water temperatures and facilitate upstream migration of adult sockeye salmon in August, also corresponds to the end of juvenile Chinook salmon migration. The general trend on the Nechako River is for increasing flows to correspond with a decrease and eventual termination of migration of Chinook salmon.

Despite the negative coefficient, increasing flows probably provide benefits such as an increased rate of migration as suggested by other studies. Given that smolts from the Nechako River must migrate approximately 1,000 km to reach saltwater (Figure 1), it is reasonable to expect an earlier start date than for populations with shorter migration routes. Delaying migration to coincide with the peak in freshet flows may ultimately result in arrival to the marine environment outside of the peak smolting period (smolt window). Although the negative value assigned to the flow variable suggests flow may play a role in the termination of migration and that early high flows would shorten the migration window, there is no support for this argument in the literature. Instead, augmentation of flow during the migration period has been recommended as a means of facilitating migration (Muir et al. 1994; Connor et al. 2003). However, fish counts from the Nechako River show that increasing flows coincide with decreasing migrant numbers. Further study is needed to determine a causal relationship, but if increased flows do serve as a cue for the termination of migration, a management strategy that includes a historically unnatural increase in discharge may have an adverse effect.

Accumulated Thermal Units

The role of ATU in migration was best described by a quadratic equation. For both models, the linear portion was assigned a positive value, while the squared portion was assigned a negative coefficient; thus, the quadratic equation captured both the increase and decline in migration despite the continuous rise of ATU over the summer. This finding corresponds to physiological studies that found that while increased temperature will accelerate the changes associated with smolting up to a point (McCormick et al. 1999; Shrimpton and McCormick 2003), it will also result in a more rapid reversion of the parr–smolt transformation (McCormick et al. 1997; Handeland et al. 2004). Associated with accelerated physiological changes, several studies have also shown that warmer temperatures result in earlier migration. Specifically, Roper and Scarnecchia (1999) found that during a 4-year study on Chinook salmon smolts, higher average spring temperatures were associated with earlier emigration dates from an Oregon river system. Likewise, McCormick et al. (1999) found that wild populations of Atlantic salmon from warmer southern rivers migrated earlier than populations from cooler northern rivers. These studies also showed that at lower temperatures, the smolting process takes longer and the migration window is extended. The coefficients from our models are in agreement, suggesting that in a cool year it would take longer to reach the negative ATU threshold, thus, extending the migration period. A threshold temperature has been suggested to be a stimulus for migration for salmon smolts (Solomon 1978; Raymond 1979); however, recent studies have shown that temperature experience may be a more important determinant for migration timing. Zydlewski et al. (2005) showed that in a controlled experiment involving manipulated temperature regimes, initiation and termination of downstream movement of Atlantic salmon smolts occurred at significantly different temperatures, but at the same ATU. Sykes (2007) had a similar finding in a laboratory experiment on Chinook salmon; a combination of ATU with the physiological indicator of smolting, gill Na^+, K^+ -ATPase, was most strongly linked to movement using a logistic regression model. While increased ATU accelerates the development and loss of physiological smolt characteristics (McCormick et al. 1997), our model results suggest a similar influence on the behavioral aspects of smolting.

Flow and ATU

Our models indicate that high flow and warmer temperatures are correlated with a decline in migration,

and a shorter migration period was found in years with high ATU and high flow. Correspondingly, delayed migration was seen in cooler low-flow years. Although these trends are not conclusive due to the relatively small sample sizes, they do indicate that for the Nechako River population of Chinook salmon, changes in temperature and flow can affect migration timing and support the need for management strategies that coincide with the prevailing hydrograph of the system.

Previous work has also found that migration is delayed in cooler low-flow years (Raymond 1979; Achord et al. 1996). As in the present study, in general peak migration also occurs before the peak flows (Raymond 1979). Temperature experience, therefore, appears to be the primary determinant of migration timing for smolts and the role of flow is secondary. Additionally, McCormick et al. (1998) reported that current does not appear to be involved in initiation of migration. Further, in a controlled laboratory study, Sykes (2007) showed that current speed had no effect on the rate of physiological change and concluded that flow will not advance smolting in the absence of a temperature increase. The role of current once migration has been initiated, however, may increase in importance. Studies have shown that active migration results in a continued development of smolt characteristics. In particular, Zaugg et al. (1985) found that gill Na^+, K^+ -ATPase activity continued to increase after release when compared with smolts that were maintained in a hatchery, suggesting a promotion of smolt characteristics and seawater tolerance with downstream migration. Lack of flow slows the rate of migration and there is an increased tendency for smolts to revert to parr and remain in freshwater for an additional year (Raymond 1979).

Relationship to Spawner Number

Our count model showed that before 1998, the model overpredicted the number of Chinook salmon migrants, but after 1998 there was an average underprediction of Chinook salmon smolts. Thermal experience (ATU), flow, and the number of spawners were included as variables in the top-ranked count model and the most parsimonious binary model (Table 1). The number of ocean-type Chinook salmon smolts migrating from an Oregon stream was found to be proportional to the number of spawners (Roper and Scarnecchia 1999). The relationship between spawner density and number of migrating stream-type Chinook salmon smolts, however, has not been as strongly defined. Downstream movement of parr in the summer and fall has been documented in a number of stream-type populations (upper Fraser River: Bradford and Taylor 1997; Snake River: Bjornn 1971; Achord et al.

2007). Chinook salmon fry vary in their tendency to move downstream (Bradford and Taylor 1997), but factors that have been linked to the magnitude of movements downstream are stream discharge, temperature, and habitat availability (Bjornn 1971). Appreciable numbers of fry also move downstream in the Nechako River (NFCP 2005); the number of migrating smolts past the Diamond Island rotary-screw traps is commonly 2–15% of the number of fry that move downstream. Estimates of parr survival to the smolt stage are not available for the Nechako River, so it is not possible to determine what proportion of smolt production is linked to the parr that migrate downstream the year before smolting. There does not appear to be any relationship between proportion of fry that move downstream and spawner number. Consequently, the differences that we found between our predicted and actual number of Chinook salmon smolts may be partially related to variability in downstream movement of fry.

Our model, however, does support a positive relationship between number of migrating Chinook salmon smolts and spawner abundance (Table 2). The number of juvenile Chinook salmon captured from 1992 to 1997 was significantly lower than for 1998–2004 and the number of spawners was significantly greater during the 1998–2004 period. We suggest that the relationship between migrating smolts and number of spawners supports the validity of our count model. Although, we did not intercept all the Nechako River Chinook salmon smolts produced from this system, our objective was to relate the timing of smolt migration to changes in environmental variables. To achieve our objective we intercepted migrating smolts at a point less than 100 km below the furthest upstream spawner location, limiting the number of migrants we intercepted, but precluding us from trapping multiple stocks that would probably comingle and that may represent different temporal trends for migration. Spawner number also had an effect on the binary model with probability of migration increasing with spawner number. It is likely that more spawners resulted in more migrants (consistent with the Count model) and, therefore, a greater probability of fish moving on a given day. A larger number of spawners would also be expected to result in a protracted migration period due to the larger pool of smolts, which is consistent with a positive relationship between probability of migration and spawner number.

Management Implications

Flow manipulations that change the timing, duration, or magnitude of increases of temperature and flow in spring could have adverse effects for the migration

behavior of Chinook salmon. For the population of Chinook salmon we studied, temperature experience (ATU) was more strongly linked to migration than was a daily or threshold temperature. In addition, both types of models showed that earlier warmer temperatures resulted in an earlier start to migration. Alternatively, while flow may not be a cue for the onset of migration, it does potentially play an important role once migration is underway and may even serve as a termination cue. Thus, managers of water resources should consider both variables when making decisions that will influence the timing and volume of water. This is particularly true in managed systems where it is possible to manipulate one variable independently of the other (e.g., release a small volume of cold water from deep in the reservoir to reduce temperature without influencing discharge). While such actions might appear to be a good strategy for addressing high water temperatures during summer, the results of this study and others show that most ecological processes are controlled by more than one variable. In addition to planned manipulations, managed systems experience unexpected events such as emergency spilling when reservoirs are too full. In these situations, the increased discharge would not result in an earlier smolting response as the required photoperiod cue would not have been received and ATU will probably be lower than in a normal flow year. However, flows that are many times higher than normal may force fish downstream months before the normal onset of migration. The temporal patterns of both water temperature and flow are important considerations for maintaining salmonid populations on flow-controlled rivers with multiple resource values.

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