ARTICLE

Geographic variation in environmental factors regulating outmigration timing of coho salmon (*Oncorhynchus kisutch*) smolts

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Abstract: The environmental cues that regulate smoltification and trigger downstream movement by salmon should vary across space in response to differences in the predictability of favorable conditions for migration and ocean entry. To examine this, we modeled the short-term outmigration probability of four coho salmon (*Oncorhynchus kisutch*) populations in three distinct geographic regions in relation to photoperiod, temperature, streamflow, lunar phase, and interactions among these variables. For smolts in Deer and Flynn creeks, Oregon (1960–1972), migration probability was influenced by numerous factors, including photoperiod, temperature (absolute and change), flow (absolute and change), and lunar phase, with certain factors interacting. Smolts from Carnation Creek, British Columbia (1972–1986) responded to a similarly diverse suite of factors (excluding lunar phase), though in somewhat different ways. In contrast, migration timing of smolts in Sashin Creek, Alaska (1959–1969) was best explained by a model that included only photoperiod, temperature, and the interaction between these terms. These population differences suggest fundamental differences across regions in the selection processes operating in both marine and freshwater environments.

Résumé : Les signaux du milieu ambiant qui régulent la smoltification et déclenchent le déplacement vers l'aval des saumons devraient varier dans l'espace en réponse à des différences sur le plan de la prévisibilité des conditions favorables à la migration et à l'entrée en mer. Pour examiner cette question, nous avons modélisé la probabilité à court terme de la migration vers la mer pour quatre populations de saumons cohos (*Oncorhynchus kisutch*) dans trois régions géographiques distinctes par rapport à la photopériode, à la température, au débit, à la phase de la lune et aux interactions de ces variables. Pour les saumoneaux dans les ruisseaux Deer et Flynn (Oregon, 1960–1972), la probabilité de migration était influencée par de nombreux facteurs dont la photopériode, la température (valeur absolue et variation), le début (valeur absolue et variation) et la phase de la lune, certains facteurs interagissant entre eux. Les saumoneaux dans le ruisseau Carnation (Colombie-Britannique, 1972–1986) réagissaient à un ensemble semblable de facteurs (hormis la phase de la lune), bien que de manière un peu différente. En revanche, un modèle n'incluant que la photopériode, la température et l'interaction de ces deux termes est celui qui explique le mieux le moment de la migration des saumoneaux dans le ruisseau Sashin (Alaska, 1959–1969). Ces différences selon la population reflèteraient des différences fondamentales selon la région dans les processus de sélection qui s'opèrent dans les milieux marins et d'eau douce. [Traduit par la Rédaction]

Introduction

The smolting and downstream migration of anadromous salmonids mark a critical phase in the life histories of these species. Most individuals within a population typically migrate over a period of a few weeks to a few months. The timing of these movements is believed to be adapted to coincide with favorable conditions for growth and survival in the marine environment (Antonsson and Gudjonsson 2002; Davidsen et al. 2005; Spence and Hall 2010) or along the migration pathway. Such synchronous movements involve complex interplay between the physiology of the organism and various environmental factors that both influence developmental state and initiate migratory behavior (reviewed in Hoar 1988 and McCormick et al. 1998). This complexity is heightened in salmon and other anadromous species because movement from hypo-osmotic freshwater environments to hyperosmotic marine waters requires dramatic changes in osmoregulatory function.

A substantial literature exists regarding both the physiology of the parr–smolt transformation and environmental factors that both regulate this transition and trigger downstream movement. Several syntheses of this literature (Wedemeyer et al. 1980; Hoar 1988; McCormick et al. 1998) have led to a widely accepted conceptual model for the migratory process (Fig. 1). The process can be divided into two phases: a preparatory phase, during which juvenile fish undergo physiological, morphological, and behavioral changes that preadapt them for life in the marine environment, and a migratory or releasing phase when fish begin moving downstream (Antonsson and Gudjonsson 2002). Environmental factors play major regulatory roles during both of these phases. Evidence from laboratory studies indicates that photoperiod entrains the natural endogenous surge in neuroendocrine activity that occurs during the preparatory phase (Hoar 1988; McCormick et al. 1998), though water temperature can mediate the rate of physiological response to changing photoperiod (Sigholt et al. 1998; McCormick et al. 2000; Zydlewski et al. 2005). Similarly, a broad range of environmental "releasing factors" have been shown or hypothesized
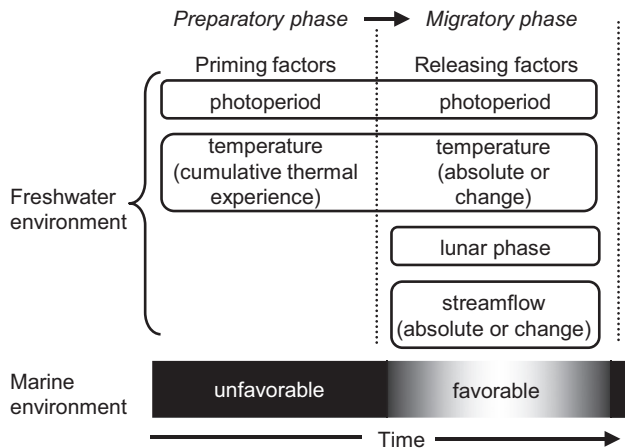
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Fig. 1. A conceptual model of environmental factors that potentially influence migration timing of salmonid smolts.

Fig. 2. Map showing location of four study populations in relation to ocean production domains of the northeast Pacific Ocean.


to trigger downstream movement of salmonids, including water temperature (Solomon 1978), change in water temperature (Jonsson and Ruud-Hansen 1985; Hvidsten et al. 1995), stream discharge or water level (Hvidsten et al. 1995; Byrne et al. 2004), change in stream discharge or water level (Hvidsten et al. 1995; Byrne et al. 2004; Davidsen et al. 2005), and lunar phase (Grau et al. 1981; Grau 1982) or position (DeVries et al. 2004).

Although all of the above environmental factors have been shown to influence migration physiology or timing in one or more salmonid species or population, it is evident from the published literature that the dominant factors regulating outmigration timing vary among populations within a species. This variability is not surprising given the broad range of ecological conditions (freshwater, estuarine, and marine) that exist across each species' geographic range and the expectation that populations should be adapted to local conditions (Jensen et al. 2012). A potentially important driver in the adaptive response of smolts to freshwater cues is the timing and predictability of favorable conditions in the marine environment. Hvidsten et al. (1998) observed latitudinal gradients in time of ocean entry of five Atlantic salmon (*Salmo salar*) smolt populations along the coast of Norway and concluded that peak timing was adapted to occur when ocean temperatures reached 8 °C, which they suggested was optimal for feeding and osmotic regulation. Similarly, Antonsson and Gudjonsson (2002) observed among-population differences in the timing of outmigration of Atlantic salmon smolts in Iceland, with migrations in northern populations corresponding to a narrow range of sea-surface temperatures. In both of these studies, the authors concluded that populations in different regions relied on different cues to arrive at sea when conditions were most favorable.

Spence and Hall (2010) recently demonstrated substantial regional variation in the patterns of outmigration of coho salmon (*Oncorhynchus kisutch*) smolts across their North American range. Specifically, they found distinct latitudinal clines in the seasonal timing, duration, and interannual variability in outmigration timing, with populations in the northern part of the range exhibiting later, shorter, and more predictable migrations than those in the southern part of the range. These patterns suggest adaptation to regional differences in timing and predictability of favorable marine conditions and, potentially, the dominant environmental cues that trigger outmigration. In the present study, we modeled relationships between environmental priming and releasing factors (photoperiod, temperature, flow, lunar phase) and migration timing of coho salmon smolts from four streams representing three distinct geographic regions along the west coast of North America. Our primary goal was to examine the relative importance of different factors in determining migration timing in
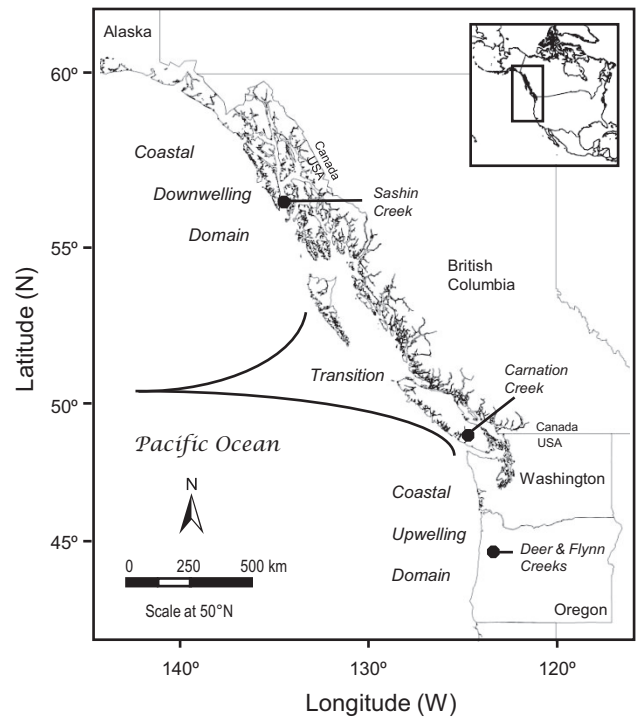
populations that enter into substantially different marine environments.

Methods

Study sites

Four coho salmon populations entering three different oceanic domains of the northeast Pacific Ocean (Favorite et al. 1976; Ware and McFarlane 1989) were modeled: Flynn and Deer creeks, Oregon, which enter the Coastal Upwelling Domain; Sashin Creek, Alaska, which enters the Coastal Downwelling Domain; and Carnation Creek, British Columbia, which enters the Transition Zone between these domains (Fig. 2). These particular streams were chosen based on the availability of long-term (≥7 years) records of downstream migrant trapping data, coupled with key environmental data. Additionally, these populations exhibited distinct differences in outmigration characteristics, including the timing of peak migration, interannual variation in peak timing, and the typical duration of the migration (Spence and Hall 2010) (Table 1).

Flynn and Deer creeks are two headwater tributaries to Drift Creek, which empties into Alsea Bay on the central coast of Oregon. From 1959 to 1973, these streams were studied as part of the Alsea Watershed Study, which examined effects of logging on stream characteristics and fish populations. Carnation Creek flows into Barkley Sound on the west side of Vancouver Island, British Columbia, and from 1971 through 1989 was likewise the site of intensive studies of the effects of logging on anadromous fish populations. Sashin Creek empties into Little Port Walter Bay, on the east side of Baranof Island in southeastern Alaska. This is the site of a long-term investigation of pink salmon (*Oncorhynchus gorbuscha*) populations; however, downstream migrant traps allowed enumeration of coho salmon smolts for 7 years during the period 1959 to 1969. For all four sites, daily records of stream discharge, water temperature, and number of outmigrating smolts were available. Summaries of physical characteristics of each watershed and stream as well as sources for further information

Table 1. Summary of outmigration timing (median date of migration), duration (mean interquartile and 90% migration interval), and variability in peak timing (standard deviation of peak migration date) of smolt migrations from four study watersheds.

Population	Years	Median date of migration	Mean interquartile range (days)	Mean time from 5% to 95% cumulative migration (days)	Avg. standard deviation of peak date (days)
Flynn Creek	14	31 March	29.8	72.9	12.4
Deer Creek	14	30 March	36.1	82.6	12.1
Carnation Creek	16	3 May	19.3	50.2	5.2
Sashin Creek	7	27 May	9.6	29.9	7.9

regarding study sites, silvicultural treatments, and data collection are provided in Table 2.

All four watersheds are relatively small (~200–1000 ha), and spawning and rearing habitat is limited to a few kilometres of stream (Table 2). The Deer Creek and Flynn Creek watersheds are subwatersheds in the larger (122 126 ha) Alsea River basin; thus, coho smolts from these streams likely represent local breeding groups within the larger Alsea River population (Lawson et al. 2007). Traps in Carnation and Sashin creeks were situated near tidewater and thus sampled fish produced throughout these watersheds. Scale analysis of returning adults indicates that most (>97%) smolts from Deer and Flynn creeks emigrate at age 1 (Moring and Lantz 1975). In Carnation Creek, age-1 and age-2 smolts were about equally abundant prior to the onset of logging, but the percentage of age-1 smolts increased to ~80% in the years after logging commenced (Holtby et al. 1989). Age structure for Sashin Creek smolts was not available but likely consists of both age-1 and age-2 smolts, as is common for populations in Alaska (Sandercock 1991).

Smolt counts and environmental data

Coho salmon smolts were enumerated daily (usually in the morning) during the period of smolt migration at weirs in each of the four study streams (Table 2). On occasion, traps in Flynn and Deer creeks were not checked for a day or two (almost always during periods of limited movement); in these instances, the total number of migrants in the trap was divided by the number of sampling days to obtain an average daily count. Minimum and maximum water temperatures were recorded daily at each site (Table 2). Mean daily temperature, which was used for modeling, was estimated by averaging the minimum and maximum daily temperatures. Daily photoperiod (time between sunrise and sunset) and fraction of moon illuminated were calculated for each site and date based on US Naval Observatory data (US Naval Observatory 2005, 2010).

Statistical model

To estimate the proportion of migrating smolts over time at each site, we fit observed counts of migrating smolts to site-specific binomial generalized linear mixed models with a logit link function (logistic-normal models). We assume the observed number of migrating fish in the ith time step (y_i) follows a binomial distribution with sample size n_i and migration probability π_i. Sample size (n_i) is the number of potential migrants remaining at time step i, defined as the total number of observed migrants in a given year and location minus the cumulative number of observed migrants through time step $i - 1$. Migration probabilities in each time step are independent, a simplifying assumption, and conditional on a vector of explanatory variables, $\boldsymbol{x}_i$. Logit-transformed migration probabilities are modeled as a linear combination of explanatory variables, plus a normally distributed random variable, $\varepsilon_i \sim N(0, \sigma^2)$.

$$(1) \qquad \log\left(\frac{\pi_i}{1 - \pi_i}\right) = \boldsymbol{x}_i^T \boldsymbol{\beta} + \varepsilon_i$$

Addition of the observation-level random effect (ε) allows for extra-binomial variability in the data (overdispersion) given the model structure and reduces the potential for underestimation of standard errors relative to a simple binomial model. Coefficients of the linear predictor, $\boldsymbol{\beta}$, and the variance of the random effect (σ^2) were estimated using the function "glmer" in the package "lme4," available for the R language–environment (R Development Core Team 2011).

Model variables

Outmigration probability was modeled at a 2-day time step. We chose this interval over a daily time step to limit the frequency of observations where smolt counts were zero or near zero, a condition referred to as "sparseness" (McCullagh and Nelder 1989). Sparseness was also a consideration in selecting starting dates (i.e., fixed dates for the first time interval) and ending dates for each stream. Starting dates were 1 February for Deer and Flynn creeks, 14 March for Carnation Creek, and 23 April for Sashin Creek. In all cases, occasional fish were trapped prior to these dates; however, the selected dates represent when fish typically began moving downstream on a consistent (i.e., almost daily) basis. For each year and stream, an end date was set as the date on which <50 eventual migrants remained in the stream.

Covariates in the model were chosen to examine effects of photoperiod, lunar phase, stream flow, change in flow, temperature, and change in temperature during the migration window, as well as the effect of cumulative thermal experience prior to migration (Table 3). For photoperiod, fraction of the moon illuminated, and temperature, we used mean daily values of these variables over the 2-day interval. Stream flow exhibited a skewed distribution and was thus ln-transformed. Degree-days was constant for any given year and was simply an additive term to assess whether temperatures prior to the onset of migration explained additional variation in migration probabilities beyond that explained by temperatures during the migration window proper. All variables in the model were expressed as deviations about their means to alleviate multicollinearity between main effect terms and associated interactions (Neter et al. 1983).

Model selection

We identified useful predictors of smolt migration at each site by first constructing a candidate set of models, then calculating model weights based on the Bayesian information criterion (BIC; Schwarz 1978; Link and Barker 2006). Considerable time was spent developing the set of candidate models, beginning with identification of seven environmental variables that have shown potential to affect the probability of smolt migration. Eleven two-way interaction terms and one squared term (photoperiod) were identified as potentially biologically relevant and evaluated for each location (Table 3). Interactions were limited to second-order terms.

Candidate models for each location were developed in four subsets, aimed at balancing parsimony and realism. The first subset always included the "full" model (containing all variables and relevant higher-order terms) and an intercept-only model for comparison purposes. To fully explore the set of relatively complex,

Table 2. Characteristics of the four study streams, watersheds, and coho salmon smolt populations.

	Study sites			
	Flynn Creek, Oregon	Deer Creek, Oregon	Carnation Creek, British Columbia	Sashin Creek, Alaska
Years of study	1960–1972	1960–1972	1972–1986	1959–1963, 1968–1969
Latitude (°N)	44.54	44.53	48.92	56.38
Longitude (°W)	123.85	123.88	125.00	134.65
Watershed area (ha)	202	303	1000	1000
Stream length upstream of trap accessible to coho salmon (km)	1.4	2.3	3.5	1.1
River km from trap to ocean	~37	~37	<0.1	<0.1
Elevation range (m)	~158–427	~171–505	~5–935	~6–799
Mean precipitation (cm)	~250	~250	~250–350	~587
Dominant form of precipitation	Rain	Rain	Rain	Mixed rain–snow
Mean water temperature (°C)	9.7[a]	9.6[a]	6.3–7.9[b]	5.7
Water temperature range (°C)	2.2–16.6[a]	1.1–16.1[a]	<1.0–17.0	−1.1–17.8
Minimum streamflow ($m^3 \cdot s^{-1}$)	0.005[a]	0.009[a]	0.02	0.30
Maximum streamflow ($m^3 \cdot s^{-1}$)	3.9[a]	5.7[a]	65.0	34.0
Dominant overstory vegetation	Douglas-fir, *Pseudotsuga menziesii*; red alder, *Alnus rubra*	Douglas-fir	Western red cedar, *Thuja plicata*; western hemlock, *Tsuga heterophylla*; Douglas-fir; Sitka spruce, *Picea sitchensis*; red alder	Western hemlock, Sitka spruce
Land use	No timber harvest	25% patch-cut with buffers in 1966	41% clear-cut from 1975 to 1981	No timber harvest
Mean coho smolt count (range)	625 (138–1273)	1784 (694–2962)	3005 (1521–4630)	1834 (1258–2865)
Avg. median date of smolt migration (avg. interquartile)	30 March (15 March–14 April)	29 March (12 March–15 April)	9 May (29 April–19 May)[c]	30 May (25 May–4 June)
Source of smolt data	J.D. Hall, Oregon State University, unpublished data	J.D. Hall, Oregon State University, unpublished data	L.B. Holtby and J.C. Scrivener, Pacific Biological Station, Fisheries and Oceans Canada, unpublished data	Olson and McNeil 1967; R. Crone, Northern Southeast Regional Aquaculture Assoc., Sitka, unpublished data
Source of environmental data	US Geological Survey (USWEST Optical Publishing 1988)	US Geological Survey (USWEST Optical Publishing 1988)	L.B. Holtby and J.C. Scrivener, Pacific Biological Station, Fisheries and Oceans Canada, unpublished data	Olson and McNeil 1967; Vallion et al. 1981
Source for watershed descriptions	Moring and Lantz 1975; Hall and Stednick 2008	Moring and Lantz 1975; Hall and Stednick 2008	Hartman et al. 1982, 1987, 1996	Crone and Bond 1976; Olson and McNeil 1967; Vallion et al. 1981

[a]Values for the pre-logging period of the Alsea watershed study (1959–1965).

[b]Two values indicate pre- and post-logging averages, as estimated from cumulative thermal sums presented in Hartman et al. (1987). Based on temperature data from 1971 through 1984.

[c]Values are for pre-logging years; migration timing was advanced following logging by approximately 1 week (Holtby 1988).

Table 3. Definitions of main effect terms and rationale for interaction terms tested in logistic-normal regression models of smolt migration probability.

Main effect terms	Variable definition
Photo	Mean photoperiod (hours from sunrise to sunset) during the ith time interval
Lunar	Mean fraction of lunar surface illuminated during the ith time interval
Temp	Mean temperature during the ith time interval
ΔTemp	Difference in mean temperature between time intervals i and $i-1$
Degree-days	Cumulative degree-days in the 60 days prior to first time interval (see text for starting dates)
Ln(flow)	Natural logarithm of mean discharge for the ith interval
ΔFlow	Maximum 1-day increase in flow between interval i and interval $i-1$

Interaction and higher-order terms	Rationale
Photo²	Response rate of fish to increasing photoperiod may decrease near the end of the migration period
Photo × temp; photo × Δtemp; photo × ln(flow); photo × Δflow; photo × lunar	Response of fish to other main effect variables may depend on photoperiod (i.e., how early or late the event occurs during the migration window)
Temp × Δtemp	Response of fish to a short-term change in temperature may depend on absolute temperature or vice versa
Ln(flow) × Δflow	Response of fish to change in stream flow of a particular magnitude may depend on absolute flow (i.e., if flows are already high, the response to a further increase may be less)
ΔFlow × lunar	Response of fish to a rapid change in stream flow may depend on lunar phase
Temp × ln(flow)	Response of fish to flow may depend on temperature or vice versa
Temp × Δflow	Response of fish to a rapid change in flow may depend on temperature
Temp × lunar	Response of fish to temperature may depend on lunar phase or vice versa

high-dimension models, we added (*i*) the full model minus each interaction term, (*ii*) the full model missing pairwise combinations of interaction terms, and (*iii*) the full model minus each main effect term and all related interactions.

The second subset in each candidate set focused on models of intermediate dimension, beginning with all possible combinations of main effects terms, plus the squared term for photoperiod. To this subset we added models containing all main effects terms, plus up to two interaction terms.

After examining results from the first and second subsets, a third subset, unique to each location, was developed based on the current BIC-best model. The exceptions were Deer Creek and Flynn Creek, which were evaluated using the same candidate sets. These two locations were assumed to have similar environmental cues because of their physical proximity, and therefore the candidate sets for both locations were identical (1125 models), but evaluated separately using each location's data. The candidate sets for Sashin Creek (1084 models) and Carnation Creek (1082 models) were unique to those locations. Based on preliminary results for each of the four creeks, covariates in the current BIC-best model that were not significant based on analysis of deviance tables were dropped, and interactions involving highly significant terms were added, to determine if these adjustments improved the model selection criterion.

The final subset in each candidate set was constructed to fully explore the space of parsimonious models at each location. All possible models having at most eight parameters (including the intercept and variance of the random effect) were evaluated to determine if a simple model would be better supported by the data. This subset was restricted to models having at least one interaction term to avoid overlap with the main effects models considered in the second subset.

After fitting each location's data to the final candidate set, we used the BIC for each model to calculate BIC weights, w_i (Link and Barker 2006)

$$(2) \qquad w_i \approx \frac{\exp(-\Delta_i/2)}{\sum_j \exp(-\Delta_j/2)}$$

where Δ_i is the difference between the BIC for model i and the minimum BIC value in the candidate set. We assume uniform prior probabilities for all models (Link and Barker 2006).

We evaluated population-level differences in environmental factors affecting smolt migration using a variable selection approach that accounts for model uncertainty (Burnham and Anderson 2002). As a relative measure of importance of each covariate to predictions of smolt migration probabilities, we summed the BIC weights of all models in which a given term appeared and compared sums across locations. These sums of "Akaike weights" (Burnham and Anderson 2002) compare the importance of each variable among populations, without having to select a single "best" model. The latter approach may provide reasonable predictive accuracy, but risks assigning zero importance to variables of lesser, but nontrivial, importance. In addition to quantifying the weight of evidence for each variable within a location, this approach also illustrates how the relative importance of each independent variable differs among locations. Because of the large number of models in the candidate sets, we limited this analysis to the set of models making up at least 99% of the cumulative BIC weight for each location. This substantially reduces the number of models in the analysis and has little to no effect on the relative importance weights.

After identifying the best-BIC logistic model for each stream, we examined the possible importance of interannual variability in migration probabilities by incorporating year as an additional term. Specifically, we examined "variable intercept" and "variable slope and intercept" models (Raudenbush and Bryk 2002), which allowed for annual changes in the model intercept and the coefficient of the ln(flow) covariate, respectively. The variable intercept structure allows for an annual shift in migration probabilities due to unaccounted-for factors. The variable slope and intercept model was included to account for the fact that stream flow exhibits greater interannual variation than the other factors considered, which could lead to different responses to flow in years that are unusually wet or dry.

Finally, for each population, we back-transformed the logit function for the best-BIC logistic model to obtain migration probabilities for coho salmon smolts during each time interval. These probabilities were then multiplied by number of potential migrants

remaining in the stream during each interval to generate plots of predicted and observed numbers of migrants for each year.

Results

Logistic-normal models indicated that outmigration timing for each population was influenced by multiple interacting factors and that the suite of important factors differed among populations. The best-BIC model for the Flynn Creek population contained ten variables, including six main effect terms, the squared photoperiod term, and three interaction terms (Tables 4 and 5). This model suggested that migration probability of coho salmon smolts increased with increasing photoperiod (the squared photoperiod term indicated a slight decline in the rate of increase, but not actual migration probability, near the end of the migration window), decreasing lunar illumination, higher water temperatures, short-term increases in water temperature, decreasing flow (i.e., reflecting the season-long trend of decreasing flows), and short-term increases in stream flow. Significant interactions between flow and change in flow indicated the response to a rapid flow increase of a given magnitude was lower if absolute flow was already high. Interactions between temperature and both the flow and change in flow variables were also found. The next five highest-ranking models all shared the identical set of main effect terms, as well the squared photoperiod term and the ln(flow) × Δflow and temp × ln(flow) interactions, lending strong support for the explanatory power of these variables. Each of these candidate models differed from the best-BIC model by the addition or subtraction of one or two interaction terms (Table 4). Summation of the BIC weights for all models in which each covariate appeared reinforced these general patterns; the photo, photo², lunar, temp, Δtemp, ln(flow), Δflow, ln(flow) × Δflow, and temp × ln(flow) terms were all present in all 32 candidate models that accounted for 99% of the cumulative BIC weight (Fig. 3a). The temp × Δflow and photo × temp covariates received combined weights of 0.74 and 0.32, respectively. No other covariate received a combined weight >0.08. Logits of predicted and observed migration probabilities for the best-BIC model showed generally good concordance, with no obvious systematic biases (Fig. 4a). Back-transforming migration probabilities and then predicting the number of migrants during each time interval likewise showed that the model succeeded at capturing the general pattern of migration in most years (see online Supplemental Fig. S1[1]), although the model tended to underpredict migration probabilities during periods of peak migration.

For Deer Creek, the best-BIC model was similar to that for Flynn Creek, sharing all six main effect terms (photo, lunar, temp, Δtemp, ln(flow), and Δflow), the squared photoperiod term, and the ln(flow) × Δflow interaction term (Tables 4 and 5). The Deer Creek model contained two additional interaction terms not contained in the best Flynn Creek model (photo × temp and photo × Δtemp) and excluded two interactions that were important in the Flynn Creek model (temp × ln(flow) and temp × Δflow). All coefficients shared between best-BIC models for Deer and Flynn creeks had the same sign except that ln(flow) coefficient for Deer Creek was positive, though not significantly different from zero (p = 0.79; Table 5). The next three highest-ranking models shared all of the main effect terms and the photo × temp and ln(flow) × Δflow interaction terms found in the best model. Two of these models contained an additional main effect term (degree-days) but otherwise differed only in the addition or subtraction of a single interaction term (Table 4). The coefficient for the degree-day term was negative, indicating a decrease in migration probability in years when temperatures in the two months preceding the migration were warmer. Summation of BIC weights for all models again

indicated that the photo, photo², lunar, temp, Δtemp, ln(flow), Δflow, photo × temp, and ln(flow) × Δflow terms were present in all 23 candidate models that accounted for 99% of the cumulative BIC weight (Fig. 3b). There was also strong support for the photo × Δtemp interaction term (combined weight = 0.88) and weaker support for the degree-day term (combined weight = 0.40). No other covariate received a combined weight >0.05. As with Flynn Creek, logits of predicted and observed migration probabilities for the best-BIC model showed generally good concordance, with no obvious systematic biases except a slight tendency for the model to overpredict when the actual proportion of migrants was extremely low (Fig. 4b). The predicted number of migrants during each time interval likewise showed reasonable agreement with observed numbers (Supplemental Fig. S2[1]), though again the model frequently underpredicted the number of migrants during the spikes in abundance that typify migrations from the two Oregon streams.

The BIC analysis for Carnation Creek indicated that three candidate models were nearly identical in their ability to explain variation in migration probabilities (Table 4). The highest-ranked model contained nine terms, including five main effect terms (photo, temp, Δtemp, ln(flow), and Δflow) and four interactions (photo × temp, ln(flow) × Δflow, temp × ln(flow), and temp × Δflow). The second- and third-best BIC models were identical to the best-BIC model except for exclusion of the Δtemp term in one model and inclusion of the photo² term in the other. We chose the second-ranked model as the preferred model because it had virtually identical explanatory power with fewer variables (Table 5). As was the case for Deer and Flynn creeks, models generated for Carnation Creek indicated that migration probability generally increased with both increasing photoperiod and increasing water temperature through the spring. Moreover, all top candidate models indicated that fish responded positively to rapid increases in flow, but the magnitude of response diminished if stream flows were already high. However, Carnation Creek models differed from those for Deer and Flynn creeks in that migration probability of Carnation Creek smolts was negatively associated with short-term increases in temperature. Summation of BIC weights for all models indicate that photo, temp, ln(flow), and Δflow main effect terms, as well the photo × temp, flow × Δflow, and temp × Δflow interactions were included in at least eight of the top nine candidate models that made up 99% of the cumulative BIC weight and received combined weights ≥0.97. There was also strong support for the temp × ln(flow) interaction (combined weight = 0.85) and weaker support for the photo² term (combined weight = 0.45). All other covariates received a combined weight <0.02 (Fig. 3c). Logits of predicted and observed migration probabilities for the best model showed generally good concordance, although there was slightly more variability in predictions relative to other populations (Fig. 4c). The predicted number of migrants during each time interval likewise tracked the observed numbers well in most years (Supplemental Fig. S3[1]).

The best-BIC model for Sashin Creek was a comparatively simple model that included only photoperiod, temperature, and the interaction between these two terms (Tables 4 and 5). The model indicated an increase in migration probability with both increasing photoperiod and increasing temperature when each variable is held at its sample mean. The influence of temperature on migration probabilities diminished when photoperiod was long, as reflected by the negative interaction term (Table 5). The second-best model added a negative lunar phase term, suggesting an increase in likelihood of migration during period of low lunar illumination. The third-best model expanded on the best model by including three flow-related terms: ln(flow), Δflow, and the

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Table 4. Best logistic-normal regression models relating migration probability to environmental factors for four coho salmon smolt populations in North America.

Model rank	No. of variables K	Photo	Photo²	Degree-days	Lunar	Temp	ΔTemp	Ln(flow)	ΔFlow	Photo × temp	Photo × Δtemp	Photo × ln(flow)	Photo × lunar	Ln(flow) × Δflow	Temp × ln(flow)	Temp × Δflow	ΔBIC	BIC weight
Flynn Creek, Oregon																		
1	10	+	−		−	+	+	−	+					−	−	+	0.00	0.35
2	11	+	−		−	+	+	−	+	−				−	−	+	1.47	0.17
3	9	+	−		−	+	+	−	+					−	−		2.17	0.12
4	10	+	−		−	+	+	−	+	−				−	−		3.68	0.06
5	11	+	−		−	+	+	−	+			+(NS)		−	−	+	4.79	0.03
6	12	+	−		−	+	+	−	+	−		+(MS)		−	−	+	4.98	0.03
Deer Creek, Oregon																		
1	10	+	−		−	+	+	+(NS)	+	+	−			−			0.00	0.51
2	11	+	−	−	−	+	+	+(NS)	+	+	−			−			1.95	0.19
3	12	+	−	−	−	+	+	+(NS)	+	+	−		+(MS)	−			5.18	0.04
4	9	+	−		−	+	+	+(NS)	+	+				−			5.32	0.04
Carnation Creek, British Columbia																		
1	9	+				+	−	+(NS)	+	−				−	−	−	0.00	0.26
2	8	+				+		+(NS)	+	−				−	−	−	0.02	0.26
3	10	+	−			+	−	+(NS)	+	−				−	−	−	0.04	0.25
Sashin Creek, Alaska																		
1	3	+				+				−							0.00	0.33
2	4	+			−	+				−							1.46	0.16
3	6	+				+		−(MS)	+	−				−			3.21	0.07
4	4	+				+			+(NS)	−							4.03	0.04
5	4	+				+		−(NS)		−							4.66	0.03
6	4	+		+(NS)		+				−							4.93	0.03
7	6	+			−(MS)	+		−	+	−				−			4.94	0.03
8	4	+				+	−(NS)			−							5.10	0.03
9	4	+	−(NS)			+				−							5.27	0.02
10	5	+			−	+			+(NS)	−							5.52	0.02

Note: Signs indicate positive or negative associations between migration probability and the variable. "NS" indicates coefficient was not significantly different from zero at $\alpha = 0.10$. "MS" indicates coefficient was marginally significant ($0.05 < p < 0.10$). Models shown for each stream account for 75% of the cumulative BIC weight.

Table 5. Regression outputs for best-BIC models for four coho salmon smolt populations.

Variable	β	SE	Z	P
Flynn Creek				
Photo	0.9998	0.0335	29.82	<0.001
Photo²	−0.1425	0.0245	−5.82	<0.001
Lunar	−0.4548	0.0988	−4.60	<0.001
Temp	0.1908	0.0420	4.55	<0.001
ΔTemp	0.2349	0.0664	3.54	<0.001
Ln(flow)	−0.1225	0.0610	−2.01	0.045
ΔFlow	0.1323	0.0255	5.20	<0.001
Ln(flow) × Δflow	−0.0749	0.0149	−5.01	<0.001
Temp × ln(flow)	−0.2412	0.0615	−3.92	<0.001
Temp × Δflow	0.0392	0.0135	2.90	0.004
Intercept	−3.3868	0.0529	−64.03	<0.001
Deer Creek				
Photo	0.7773	0.0261	29.81	<0.001
Photo²	−0.0685	0.0178	−3.85	<0.001
Lunar	−0.2853	0.0809	−3.53	<0.001
Temp	0.1115	0.0315	3.54	<0.001
ΔTemp	0.2059	0.0490	4.20	<0.001
Ln(flow)	0.0132	0.0497	0.26	0.791
ΔFlow	0.0847	0.0157	5.40	<0.001
Ln(flow) × Δflow	−0.0613	0.0096	−6.38	<0.001
Photo × temp	0.1126	0.0211	5.34	<0.001
Photo × Δtemp	−0.1025	0.0297	−3.45	<0.001
Intercept	−3.1587	0.0462	−68.33	<0.001
Carnation Creek				
Photo	1.1847	0.0388	30.56	<0.001
Temp	0.2038	0.0267	7.61	<0.001
Ln(flow)	0.0726	0.0586	1.24	0.216
ΔFlow	0.0214	0.0042	5.03	<0.001
Ln(flow) × Δflow	−0.0110	0.0020	−5.61	<0.001
Temp × Δflow	−0.0027	0.0010	−2.72	0.007
Temp × ln(flow)	−0.0945	0.0285	−3.31	<0.001
Photo × temp	−0.1291	0.0214	−6.02	<0.001
Intercept	−2.9900	0.0515	−58.11	<0.001
Sashin Creek				
Photo	1.9418	0.1507	12.884	<0.001
Temp	0.2979	0.0563	5.293	<0.001
Photo × temp	−0.3735	0.0558	−6.689	<0.001
Intercept	−3.0896	0.1138	−27.145	<0.001

interaction between these two terms. This model accounted for 7% of the cumulative BIC weight compared with 33% for the best model (Table 4). Summation of BIC weights for all models indicated that photoperiod, temperature, and their interaction were included in all 78 models that accounted for 99% of the cumulative BIC weight. Support for effects of lunar illumination (combined weight = 0.37), ln(flow) (combined weight = 0.23), Δflow (combined weight = 0.25), and the ln(flow) × Δflow interaction (combined weight = 0.12) was substantially weaker. Combined BIC weights for all other covariates were <0.06. Logits of predicted and observed migration probabilities for the best model showed less concordance for Sashin Creek than for the other three streams (Fig. 4d). In part, this reflects the much simpler model structure (i.e., only photoperiod, temperature, and their interaction), which captures less of the short-term variation in migration probability and migrant numbers compared with the models for the other three populations (Supplemental Fig. S4[1]).

For all four study populations, models that allowed for annual changes in either the model intercept or the model intercept and coefficient for the ln(flow) covariate did not improve model fit; BIC values for these models were 23 to 90 points higher than for the best-BIC models that lacked these variables. Plots comparing predicted migration probabilities for models with and without year effects showed that the models produced nearly identical predictions except at extremely low (<0.01) migration probabilities (results not shown). This result is noteworthy since significant year effects would reduce the utility of the models for making future predictions.

Discussion

Our model results indicate that migration timing in coho salmon smolts is a complex process regulated by multiple, interacting environmental factors and that the specific set of factors governing migration varies substantially among populations. For the Deer and Flynn creek populations in Oregon, we found evidence that photoperiod, water temperature (absolute and change), stream flow (absolute and change), and lunar phase all influenced downstream migration, with responses to some variables dependent on others. For Carnation Creek, British Columbia, all of the same primary factors except lunar phase were influential, although for one variable (Δtemp) the relationship was opposite (negative) to that found for the two Oregon populations. For Sashin Creek, Alaska, migration probability was best explained by a much simpler model that included only photoperiod, temperature, and the interaction between these two variables.

The observed differences in environmental factors controlling migration in the four study populations suggest differences in the balance of selection pressures operating both along the migration pathway and in the marine environments that smolts enter. Ultimately, these differences are likely dictated by spatial variation in the timing and predictability of favorable conditions in the marine environment, with the use of specific environmental cues depending, in part, on whether they are reliable indicators of favorable ocean conditions. Other cues may serve as important indicators of favorable windows for passage downstream to the ocean, but only if the survival benefit is not offset by increased mortality after ocean entry. The Sashin Creek coho population, like others in southeast Alaska, enters into the Coastal Downwelling Domain (Ware and McFarlane 1989) where the optimal window of favorable marine conditions appears to occur with high predictability (Spence and Hall 2010). In this case, photoperiod likely provides a highly dependable signal for those favorable conditions. Although warmer stream temperatures did influence migration probability in this population, leading to advancement of the median date of migration in warmer years, this variation occurred over a fairly restricted time frame (i.e., a maximum of 12 days over the 7 years of record). Stream flow and lunar phase do not appear to be important migration cues for this population.

The other three study populations enter the ocean in the Coastal Upwelling Domain (Deer and Flynn creeks) and near the southern edge of the transitional region between the Coastal Downwelling and Coastal Upwelling domains (Carnation Creek; Fig. 1). In these marine environments, conditions during the spring are highly unpredictable because of substantial variability in the timing of the spring transition and the strength and effectiveness of coastal upwelling (Ryding and Skalski 1999; Logerwell et al. 2003), as well as the strength of the Aleutian Low pressure system, which influences bifurcation of the Subarctic Current into the Alaska Current and California Current along the west coast of North America (Pearcy 1997). These smolt populations tend to exhibit more protracted migrations than those in Alaska (Spence and Hall 2010), which suggests that no single cue in fresh water serves to synchronize outmigration with the favorable marine window. Each of these populations responded to a number of environmental factors, including absolute flow, short-term changes in flow, absolute temperature, short-term changes in temperature, and lunar phase (Oregon populations only), in addition to photoperiod. These more complicated relationships suggest a stronger influence of selection pressures exerted along the migration pathway. For the two Oregon populations, this may

Fig. 3. Summation of BIC weights for individual variables for models accounting for 99% of the cumulative BIC weight (see text for details) for each population. Signs associated with each bar indicate whether the relationship to migration probability was positive (+) or negative (−) for those variables with BIC weights of >0.10.
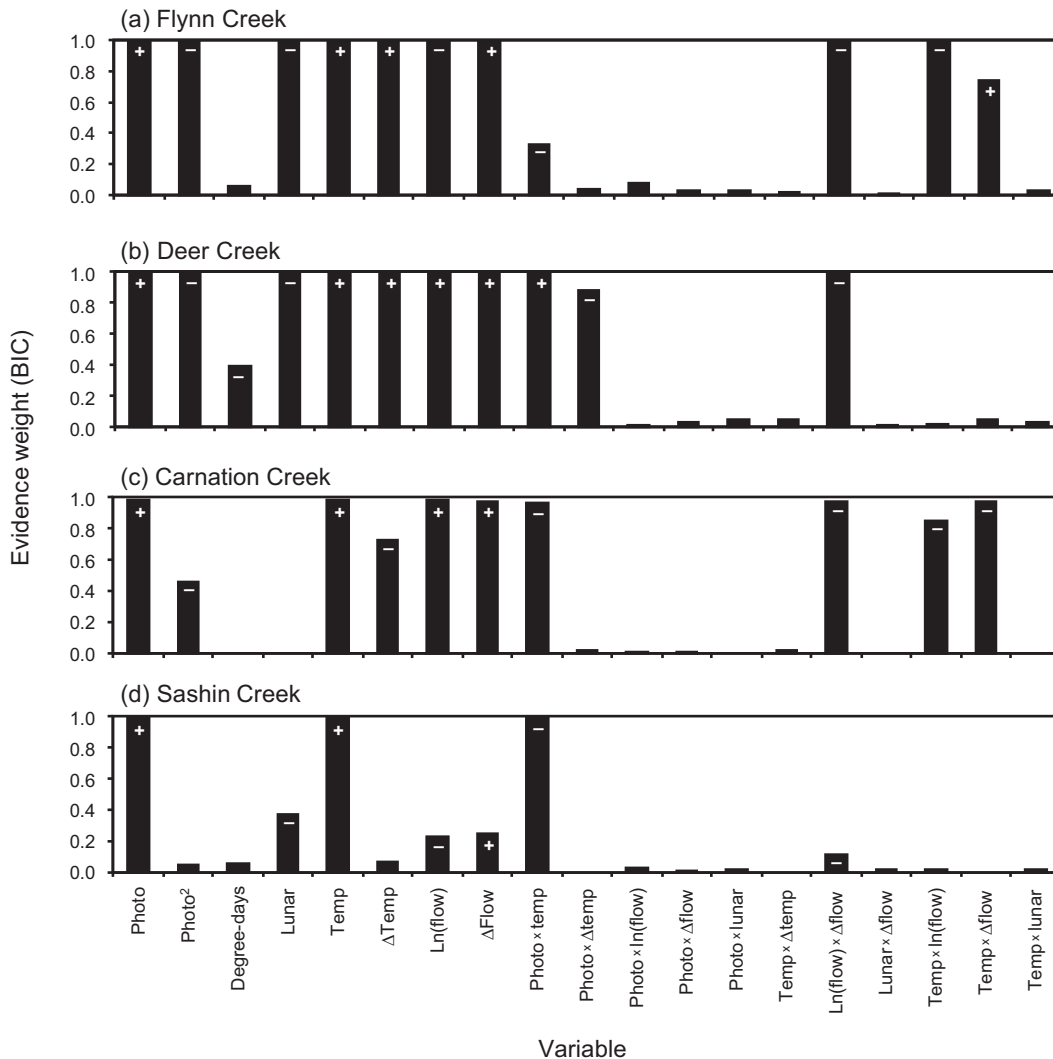
reflect, in part, the greater instream distance these fish must travel (~37 km) before reaching the ocean. In the following sections, we elaborate on the influences of individual environmental factors on migration timing in the different populations.

Photoperiod

For all four populations modeled, photoperiod was clearly an important explanatory variable, with migration probability increasing as photoperiod increased during the spring. Photoperiod has long been recognized as the key priming factor that entrains natural endogenous rhythms and synchronizes the physiological, morphological, and behavioral changes that precede smolt migration for many salmonid species (Hoar 1988; McCormick et al. 1998). Although other factors influence migration timing, it is likely that these proximate cues influence migration only during a limited temporal window (Hvidsten et al. 1995) that is dictated primarily by photoperiod (McCormick et al. 1998).

A more noteworthy finding from our study is that the rate at which migration probability increased with photoperiod differed among populations in the three regions. Direct comparisons of the regression coefficients are confounded by the significant photo² terms in the two Oregon models (Table 5). But for the remaining two populations, the difference in magnitude of coef-

ficients indicates that the Sashin Creek population showed a more rapid response to increasing photoperiod than the Carnation Creek population. This likely reflects the narrow migratory window exhibited by the Sashin Creek population versus the more protracted migration period for the Carnation Creek population. The two Oregon populations exhibited even longer migrations that typically lasted 2–3 months. These observations suggest that for these southern-most populations, either the duration of the physiological smolt window (sensu McCormick et al. 1998) is generally longer than for the Alaska population or there is greater individual variation in the response to photoperiod. Regardless, it suggests that at the population level, the nature of the physiological smolt window varies across a species' range.

Temperature

Migration probability was positively related to water temperature for all four study populations. Significant interactions between temperature and other factors in each of the models indicate that the influence of temperature can vary with these other factors. However, in general, these relationships suggest that smolts tended to migrate earlier in years when stream temperatures were warmer during the migration window. This result is consistent with studies that have shown correlations between

Fig. 4. Logits of observed versus predicted migration probabilities for coho salmon smolts in four study watersheds. For logit transformations, 0.0001 was added to the migration probability to avoid zero values (evident as the vertical line of points on the left-hand side of each plot, indicating intervals when no fish migrated). Diagonal line is the line of unity.
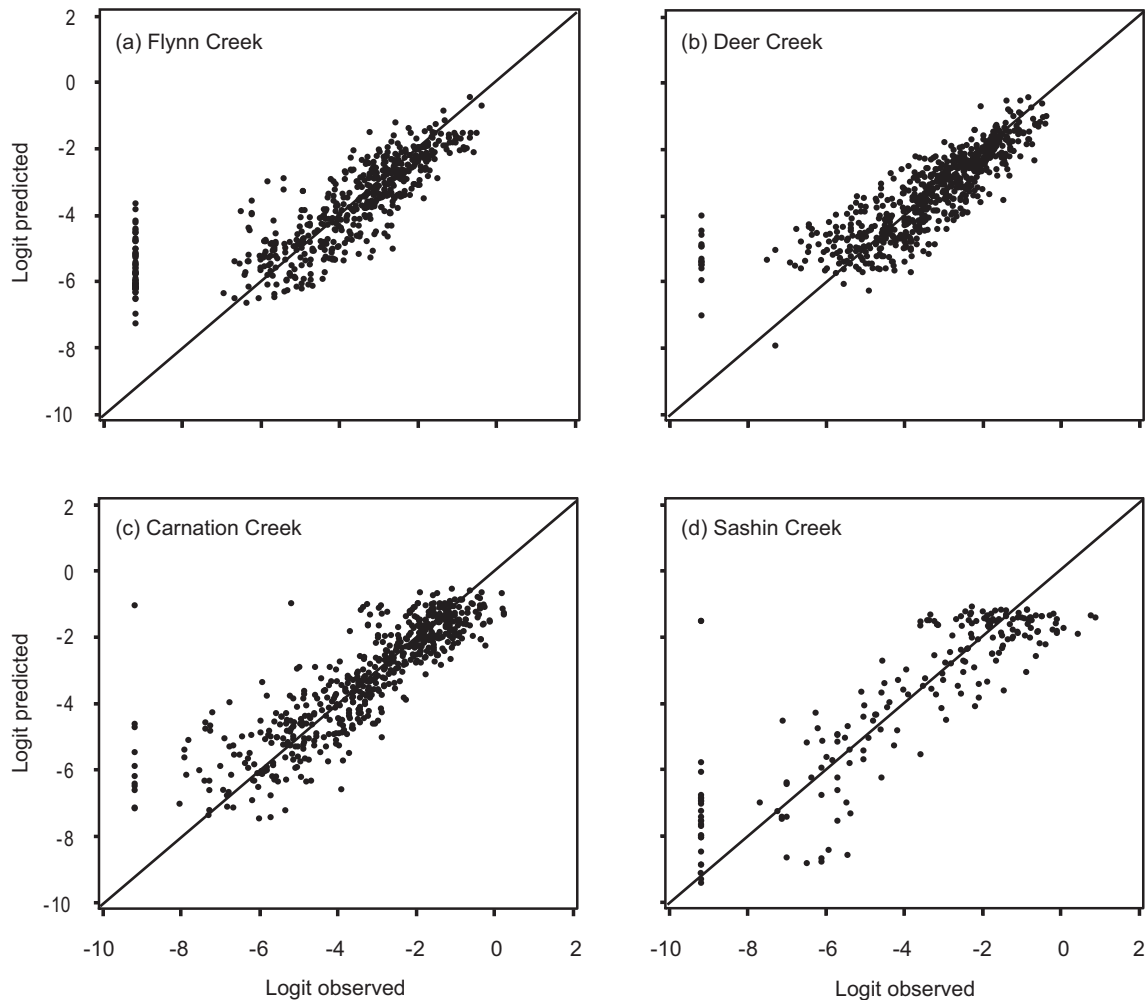

either average water temperature or cumulative thermal experience (i.e., degree-days) and median dates of migration for coho salmon (Holtby et al. 1989) and other salmonids (Bohlin et al. 1993; Roper and Scarnecchia 1999; Jonsson and Jonsson 2009), as well as studies that have linked short-term variation in the numbers or proportions of smolts to water temperature or cumulative thermal experience (Hvidsten et al. 1995; Sykes et al. 2009).

Although positive associations between migration probability and temperature were observed for all four populations, striking differences in the temperature patterns in the four streams during the primary migration period (Fig. 5) suggest that the way smolts use temperature as a cue may differ among populations. In the temperate climate of coastal Oregon, stream temperatures between February and May fluctuated over a fairly narrow range, trending upward only at a very slow rate (0.23 and 0.65 °C per month during the 90% interquantile of migration for Flynn and Deer creeks, respectively; Figs. 5a, 5b). In contrast, water temperatures during the peak of migration rose much more rapidly in Carnation and Sashin creeks (~2.1 and ~4.2 °C per month, respectively), and fish migrated over a broader range of temperatures despite migrating over a shorter time period (Figs. 5c, 5d). Consequently, temperature patterns may play a more important role than absolute temperatures, particularly in the two northern populations. It is also evident from these differing temperature patterns that there is no specific threshold temperature that initiates

migration for coho salmon in any of the four study populations. This is most clearly demonstrated for Sashin Creek. In some years, 95% of smolts migrated before mean water temperatures reached 5 °C, whereas in other years fewer than 5% of fish had emigrated when temperatures had reached 5 °C, and fish continued to migrate at temperatures exceeding 12 °C. These observations indicate that temperature is secondary to photoperiod in determining migration timing.

Short-term changes in temperature also influenced migration probability, but the relationship (positive or negative) varied among populations. Increases in temperature stimulated migration in two populations (Deer and Flynn creeks), as has been observed in certain populations of Atlantic salmon (Jonsson and Ruud-Hansen 1985) and sea-run brown trout (*Salmo trutta*; Bohlin et al. 1993). However, for Carnation Creek, the opposite relationship was observed, with migration probability increasing with short-term decreases in temperature. This difference was probably due to the fact that decreases in Carnation Creek temperatures often coincided with rainfall events that triggered downstream movement, as evidenced by a negative correlation between Δtemp and Δflow (Pearson correlation: $r = -0.26$; $p < 0.001$), which contrasts with the weak positive correlations found between these variables in Flynn Creek ($r = 0.15$, $p < 0.001$) and Deer Creek ($r = 0.09$, $p = 0.025$). Hvidsten et al. (1995) similarly found a negative relationship between change in temperature and smolt migration,

Fig. 5. Two-day running mean daily temperature during the 90% interquantile of outmigration for coho salmon smolts in (*a*) Flynn Creek, Oregon; (*b*) Deer Creek, Oregon; (*c*) Carnation Creek, British Columbia; and (*d*) Sashin Creek, Alaska.
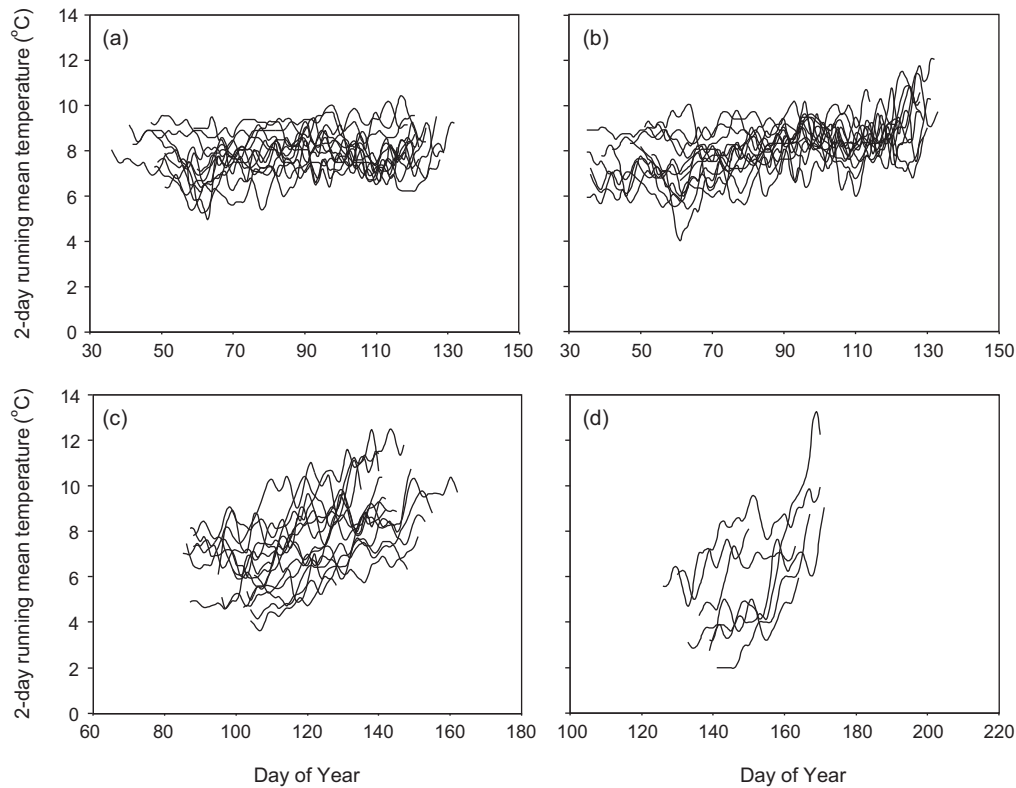
which they attributed to temperature declines associated with snowmelt-driven increases in flow.

Although temperatures during the migration period clearly affected migration probability of smolts, we found little evidence that water temperatures in the 60-day period preceding the onset of migration played a major role in determining outmigration timing for any of the four populations modeled. Only for Deer Creek did models suggest that cumulative thermal experience prior to the migration period explained variation in migration probabilities, and the result was counterintuitive, with fish showing a tendency to migrate later when temperatures prior to the migration period were warmer. Previous studies of various salmon species have found correlations between median dates of migration and degree-days or mean temperature measured over varying time periods that included weeks or months preceding the onset of migration (Foerster 1937; Jonsson and Ruud-Hansen 1985; Jonsson and Jonsson 2009), including an analysis of the Carnation Creek dataset used in our study (Holtby et al. 1989). However, most of these analyses did not independently evaluate the effects of temperature during the premigratory and migratory periods. Consequently, it is not clear whether temperatures during the migratory period alone might be adequate to explain interannual differences in the peak of migration. In our study streams, water temperatures before and during the migration period each year were positively correlated (more so in Sashin and Carnation creeks than in the two Oregon streams), so we cannot completely rule out the possibility that temperatures affected developmental rate prior to the migration period, thereby influencing subsequent migration probability. However, the more proximate effect of temperature during the migration window was a substantially better predictor of migration probability than the cumulative thermal experience in the 2 months preceding the migration for all four populations. These results support the idea that temperature increases alone are insufficient to advance smolt-

ing and migration in the absence of photoperiod cues (McCormick et al. 2002).

Flow

High water flow has frequently been cited as an important factor stimulating downstream migration of salmon smolts (reviewed in Northcote 1984; McCormick et al. 1998), although not all populations have shown strong or positive responses to flows (e.g., Jonsson and Ruud-Hansen 1985; Roper and Scarnecchia 1999; Sykes et al. 2009). Our results indicate that the response of coho salmon smolts to flow was both complicated and variable among the four populations studied. For three of the populations (Flynn, Deer, and Carnation creeks), the responses were similar overall. For Flynn, Deer, and Carnation creeks, migration probability was positively associated with short-term increases in flow caused by rainfall events; however, the response to flow increases was dependent on the absolute flow, as evidenced by significant negative interactions between ln(flow) and Δflow. If flows were already high, additional increases in stream discharge did not elicit the same response, most likely because smolts that were primed to migrate had already done so with a previous event. There were differences in the sign of the ln(flow) coefficients for these three streams (negative for Flynn Creek and positive but nonsignificant for Deer and Carnation creeks); however, we caution against overinterpreting these differences given the significant ln(flow) × Δflow interactions in each model and the expectation that smolts in Deer and Flynn creeks should respond similarly given their close proximity. Likewise, we suspect that significant interactions between temperature and both flow (negative) and Δflow (positive) for Flynn Creek but not Deer Creek reflect spurious relationships rather than meaningful differences in the factors controlling migration timing. In sharp contrast with the Oregon and British Columbia populations, we found only weak evidence

that either absolute flow or change in flow influenced migration timing for Sashin Creek coho salmon smolts.

The variable response of the four smolt populations to stream flow patterns may arise from differences in selective regimes both along the migratory pathway and in the marine environment. For the Flynn, Deer, and Carnation creek populations, migrating during periods of increased discharge may confer several advantages, including enabling smolts to traverse shallow riffle areas where risk of exposure to predators may be high (Bohlin et al. 1993), facilitating rapid movement through unfamiliar habitats (Sykes et al. 2009), and avoiding detection by visual predators owing to increased turbidity during these events (Aarestrup et al. 2002). Alternatively, increased discharge conceivably could provide a signal for favorable marine conditions. However, Lawson et al. (2004) found that wetter springs and higher mean stream flows were associated with later dates of the spring transition off the Oregon coast. Hence, the adaptive response would be to delay migration in years of higher precipitation and flow. The lack of a strong response to flow or flow changes by Sashin Creek smolts suggests either that flow is an unreliable indicator of a narrow window of favorable marine conditions or that the higher spring stream flow in this stream (4- and 10-fold higher than Carnation Creek and the two Oregon streams, respectively) is sufficient to allow safe downstream passage throughout the migration period.

Lunar phase

As with other environmental factors, the response of coho salmon smolts to the lunar cycle differed among the four study populations. Migration probability was significantly (negatively) associated with lunar phase for both Flynn and Deer creeks in Oregon, indicating an increased tendency for smolts to migrate during periods of lower lunar illumination. In contrast, evidence for a lunar influence on migration timing was weak for Sashin Creek and lacking entirely for Carnation Creek (Fig. 3; Table 4). These apparent population-level differences in the importance of lunar phase as a migration cue are not surprising given the inconsistency in findings of previous studies. Although several physiological studies have reported surges in plasma thyroxine levels during the new moon phase in several Pacific salmonids (Grau et al. 1981; Grau 1982; Yamauchi et al. 1985) and Atlantic salmon (Boeuf and Prunet 1985), others have failed to find strong evidence of relationships between thyroxine levels and lunar phase (Boeuf et al. 1989; Youngson and Simpson 1984; Lin et al. 1985). In situ investigations of the role of lunar phase on timing of outmigration have similarly produced mixed results, with some studies reporting a greater tendency for salmon smolts to migrate in the period surrounding the new moon (Youngson et al. 1983; Roper and Scarnecchia 1999) or during both the new and full moons (Hvidsten et al. 1995), but others finding no evidence of a significant lunar influence on migration timing (e.g., Jonsson and Ruud-Hansen 1985; Byrne et al. 2003; Wood et al. 1993).

The differences in response to lunar phase between coho populations in our study suggest that utility of lunar phase as a cue varies across space. In Sashin Creek, like other southeast Alaska populations, more than half of all smolts typically migrate over a period of 10 or fewer days, and the median date of migration varies little (<2–3 weeks) among years (Table 1). This suggests that migration timing is adapted to exploit a narrow and relatively fixed period of favorable ocean conditions (Spence and Hall 2010). Lunar phase would serve as a poor cue for outmigration, since the new moon will periodically occur outside the optimal ocean window. In contrast, for the two Oregon populations that did respond to the lunar cycle, smolt outmigration typically spanned a period of 2–3 months, encompassing multiple lunar cycles. Here, migrating during the new moon appears to confer advantages that are not overwhelmed by strong selection pressures to enter the sea during a specific and narrow window. The potential advantages of migrating during the new moon include decreasing the vulnerability of smolts to predators during the migration (Grau et al. 1981; Grau 1982) or, alternatively, synchronizing migration timing so that smolts arrive at estuarine environments during favorable tidal cycles (Hvidsten et al. 1995). For the Deer and Flynn creek populations, the influence of lunar phase on migration probability was limited to the new moon phase and not to the full moon, as reported for Atlantic salmon in a Norwegian river (Hvidsten et al. 1995). Post hoc analyses in which the lunar illumination term in the best-fit models was replaced with a semilunar cycle found in all cases that BIC values indicated a poorer fit. This lends stronger support for the direct linkage between light levels and predation risk, rather than between tidal cycles and subsequent survival in these populations.

Although Deer and Flynn creek smolts tended to migrate during periods of lower lunar illumination, lunar phase appeared to be less important than other proximate cues in determining migration timing. For both populations, major peaks in the number of smolts migrating from both of these streams coincided with the full moon in several of the 13 years examined (Supplemental Figs. S1 and S2[1]). In most of these instances, these peaks occurred coincident with increases in streamflow. These observations suggest that the influence of lunar cycle can be overridden by that of flow, perhaps because cloud cover and increased turbidity associated with rain events provide a predator avoidance benefit comparable to migrating during the new moon.

Implications

Population-specific differences in the cues coho salmon use to trigger outmigration will likely produce differences in how populations respond to anthropogenic changes such as climate change. Such differences will be manifest both in the immediate responses (the influence of past selection) and evolutionary responses, which will depend on genetic variability and phenotypic plasticity of populations and the rate of adaptation (Crozier et al. 2008). For the Sashin Creek population, the dominant role of photoperiod on migration timing, coupled with the lesser dependence on factors such as flow and temperature, suggest that this population may be more responsive to changes in the phenology of the marine environment than to changes that occur in fresh water. Even modest climate-induced shifts in the timing of the optimal marine window could result in a mismatch between migration timing and favorable marine conditions. Further, the comparatively limited phenotypic variation in migration timing may limit the ability of the population to track such changes.

For the Deer, Flynn, and Carnation creek populations, greater responsiveness to temperature and flow cues suggests that changes in temperature and precipitation regimes could directly influence migration timing. In these populations, climatic warming that is expected in the Pacific Northwest (Mote et al. 2003; Crozier et al. 2008) could lead to advancement in migration timing. Directional responses to flow changes are more difficult to predict because predictions of temporal patterns of precipitation are substantially more uncertain than those of temperature (Mote et al. 2003). Advancement of migration timing could be particularly detrimental to these populations if the timing of the spring transition in the Coastal Upwelling Domain is delayed as a consequence of climate change, as has been predicted (Snyder et al. 2003; Diffenbaugh et al. 2004). This could result in the smolt window and optimal marine window occurring out of phase (Crozier et al. 2008). Conversely, greater phenotypic variation in migration timing of smolts from these populations may suggest greater capacity to track such shifts. Although our analysis includes only one or two populations in each of the oceanic domains, the regional consistencies in migration patterns exhibited by many coho populations (Spence and Hall 2010) suggest that the population-specific responses we observed may occur across larger spatial scales as well.

Acknowledgements

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