

Modeling the Influence of Environmental Factors on Spawning Migration Mortality for Sockeye Salmon Fisheries Management in the Fraser River, British Columbia

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Abstract.—The impact of freshwater environmental factors on spawning migration mortality was modeled to provide a predictive tool for fisheries management of four run timing groups of Fraser River sockeye salmon *Oncorhynchus nerka*: early Stuart (Stuart Lake), early summer, summer, and late. We tested the significance of different measures of water temperature, discharge, fish abundance, and entry timing for forecasting discrepancies between lower-river and upriver escapement estimates using multiple regressions of principal component scores. Descriptive discrepancy models (i.e., “management adjustment” models) identified using Akaike’s information criterion were consistent with the known biology of each group. For example, temperature and discharge thresholds were selected for early Stuart run discrepancy models, reflecting the extremes in both variables experienced by these early migrants. Predictive discrepancy models were also generated for each run timing group by using the limited number of environmental variables that are available in-season to fisheries managers. Even predictive discrepancy models using simple environmental metrics of average river temperature, flow, and river entry timing provide a valuable tool for forecasting relative indices of spawning migration mortality. This study provides an example of how environmentally based predictive tools can be used to inform fisheries management decisions and improve the probability of achieving spawning escapement targets.

There is a growing awareness that interannual variation and trends in climate patterns can have an impact on condition and survival of fish throughout their life history and thus can impact population productivity (Beamish and Bouillon 1993; Adkison et al. 1996; Bradford and Irvine 2000; Mueter et al. 2002; Rand et al. 2006). Therefore, maintaining spawning populations may depend on our ability to provide a quantitative link between environmental factors and measures affecting productivity, including abundance, fish condition, migration success, and spawning success (Jacobson and MacCall 1995; McGowan et al. 1998; IPCC 2001; Schirripa and Colbert 2006; Keefer et al. 2008b).

Fisheries management has become more precautionary in recent years, in part because fish abundance has declined, and uncertainties in forecasts of abundance

are increasingly being recognized (Richards and Maguire 1998; Hilborn et al. 2001). A precautionary approach generally results in a reduction in exploitation rates and a decline in numerical catches unless forecasts of abundance can be improved to more accurately predict future production. Given large uncertainties in environmental effects on population productivity, rigorous model selection procedures are essential when evaluating empirical relationships and identifying predictive models. In some cases, simple regression relationships may be effective at capturing a large portion of the variability in complex biological processes while providing a useful forecasting tool to aid in fisheries management (Keefer et al. 2008a). Currently, regression models relating freshwater environmental exposure to surrogates of spawning migration mortality are being used in the management of Fraser River sockeye salmon *Oncorhynchus nerka* to reduce the uncertainty in estimates of migration success for populations (i.e., stocks) that have survived marine and lower-river fisheries. Furthermore, when combined with in-season forecasts of river environmental condi-

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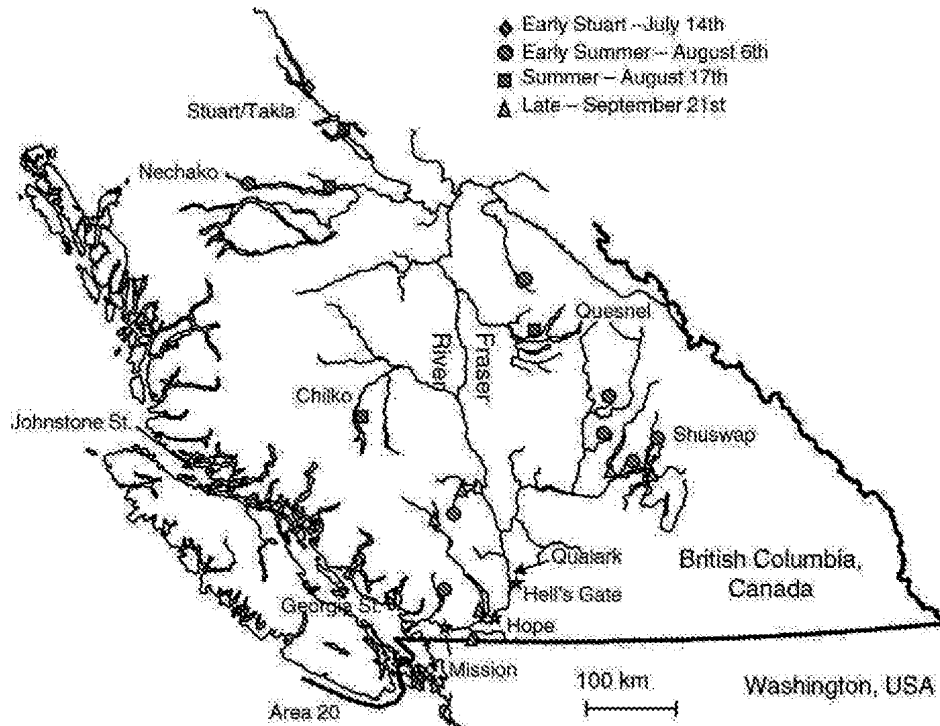


FIGURE 1.—Map of the Fraser River watershed, British Columbia, showing major spawning grounds and median Hell's Gate 50% run timing dates (indicated in the legend) for the early Stuart, early summer, summer, and late runs of sockeye salmon. Map is used with permission from Hague and Patterson (2007).

tions and migration timing, these models have been used to adjust fishing pressure to increase the probability of obtaining desired escapement targets (the target number of fish surviving to reach their natal spawning grounds). In our study, we first provide rationale for implementing environmental models, and we then use Akaike's information criterion (AIC) to identify a suite of best-fit models for Fraser River sockeye salmon.

The Fraser River sockeye salmon fishery is the largest salmon fishery in Canada, with annual catches averaging 5.5 million fish over the previous 50 years (Pacific Salmon Commission, unpublished data). The primary management goals for this fishery are to achieve spawning escapement targets while maximizing harvest. Fraser River sockeye salmon fisheries are divided into four chronological run timing groups for management: early Stuart (Stuart Lake), early summer, summer, and late. Each run timing group can offer fishing opportunities in commercial, recreational, and First Nations fisheries; these opportunities are conditional on preseason and in-season forecasts of annual abundance. Run size and timing of each run timing group are assessed in-season as fish migrate through marine areas and the lower river (Cave and Gazey 1994) near Mission, British Columbia (Figure 1),

providing essential information for balancing catch allocations and spawning escapement objectives. While Mission estimates of in-river abundance inform assessments of run size and migration timing, they do not account for additional restrictions that should be placed on catch when fish loss occurs in the Fraser River upstream of Mission. Sockeye salmon losses in the Fraser River that were large enough to cause complete run failures were first reported in Hudson's Bay Company records at Fort St. James in 1899 and 1900 (Cooper and Henry 1962). Since then, there have been numerous examples of high mortalities during the spawning migration (fish detected at Mission but failing to reach the spawning grounds; English et al. 2005; Patterson et al. 2007b) and after migration (i.e., prespawn mortalities; Gilhousen 1990). In some years, these sources of mortality account for over 90% of the total run size, representing millions of fish (Cooke et al. 2004) and millions of dollars of lost revenue (Lapointe et al. 2003).

Numerous studies have documented a relationship between mortality during spawning migration and extended freshwater residence (Cooke et al. 2004; Wagner et al. 2005; Young et al. 2006), high in-river temperatures (Macdonald et al. 2000; Naughton et al. 2005; Crossin et al. 2008; Farrell et al. 2008; Keefer et

al. 2008b), and high discharge (Macdonald 2000; Rand et al. 2006). Each run timing group experiences distinct river conditions, with a greater likelihood of extreme discharge during the early runs and extreme temperature during the summer runs (Patterson et al. 2007a). Since 1995, late-run populations have entered the Fraser River earlier, resulting in extended freshwater residence times and exposure to higher river temperature and discharge (Lapointe et al. 2003; Cooke et al. 2004). Mortality during spawning migration reduces population productivity and may hamper management strategies, such as rebuilding initiatives on depleted populations. Fishery managers who are expected to open and close fisheries based on numbers of sockeye salmon entering the river (in-season management) may find that their targets for spawning escapement and catch allocation become unattainable when extreme environmental conditions cause high mortality during spawning migration (Holt and Peterman 2006). These challenges eventually stimulated the integration of river environmental and entry timing forecasts into management models for Fraser River sockeye salmon, but these models have yet to be rigorously evaluated.

Currently, there is no direct method to measure mortality from exposure to adverse in-river environmental conditions experienced by returning Fraser River sockeye salmon (Patterson et al. 2007b). Therefore, the adopted practice is to use the discrepancy between lower-river potential spawning escapement (PSE) estimates (lower-river escapement after accounting for upriver catches) and upriver spawning ground escapement (SE) estimates (Figure 2). Escapement discrepancies can arise due to a combination of factors, including natural mortality, unreported catch, errors in catch estimates, and errors in PSE and SE estimates. Forecasts of escapement discrepancies are used to adjust harvest to account for anticipated mortality during spawning migration. These harvest adjustments, termed "management adjustments" (MAs), are applied to increase the probability of achieving escapement targets on the spawning grounds. Initially, MA models made no allowances for the possible influence of the current year's environmental conditions on migration success. Instead, managers simply applied the median escapement discrepancy associated with each run timing group. Consequently, MAs were too small in years with extreme environmental conditions (resulting in shortfalls in spawning escapements relative to the targets) or were too large when conditions were benign (resulting in foregone catch). Since 2002, observed and forecasted in-river environmental conditions and river entry timing have been included in forecasts of escapement discrepancies under the assumption that they would reduce errors in

discrepancy forecasts and thus increase the likelihood of achieving Fraser River sockeye salmon management goals (see Appendix 1 for current model structure; see also Hague and Patterson 2007).

The purpose of this study was to evaluate the use of environmental variables (e.g., river temperature, river discharge, entry timing, fish density) to forecast in-season harvest adjustments that are required to compensate for anticipated mortalities during spawning migration, thus increasing the probability of achieving management goals for Fraser River sockeye salmon. Our first objective was to identify a suite of biologically relevant and statistically significant candidate predictor variables that describe the relationship between sockeye salmon spawning migration mortality and Fraser River environmental factors. Our second objective was to develop two sets of MA models for each sockeye salmon run timing group: (1) descriptive models that explain the majority of the variation in escapement discrepancies and that are useful for simulation and postseason evaluation; and (2) predictive models subject to in-season forecasting and management constraints that can be used to provide timely forecasts of discrepancies for fishery management purposes. Although the application of these models is specific for Fraser River sockeye salmon management, the integration of ecosystem parameters into fisheries management models is broadly applicable to other locations and management systems.

Methods

Data sources.—A time series of lower- and upper-river escapement estimates (i.e., escapement estimates before and after spawning migration mortality has occurred) and in-river environmental data were available from 1977 to 2006. Lower-river escapement estimates from a hydroacoustic monitoring facility near Mission (Figure 1) were provided by the Pacific Salmon Commission. The Pacific Salmon Commission excludes data during some years to avoid potential bias in the lower-river escapement estimates (Xie et al. 2002, 2005). Acoustic estimates of sockeye salmon abundances are less accurate when the run size is small, when sockeye salmon co-migrate with large numbers of pink salmon *O. gorbuscha* (i.e., early Stuart group: 1977, 1980, 1982, 1984, and 1986; early summer group: 1993; summer group: 2002; late group: 1977, 1979–1981, 1983–1985, 1987–1989, 1991–1993, 1995, and 2005), or both. The Pacific Salmon Commission also provided information on catch rates and estimated timing of river entry for different run timing groups from the lower river, while spawning ground (upriver) escapement estimates were obtained from both the Pacific Salmon Commission (1977–

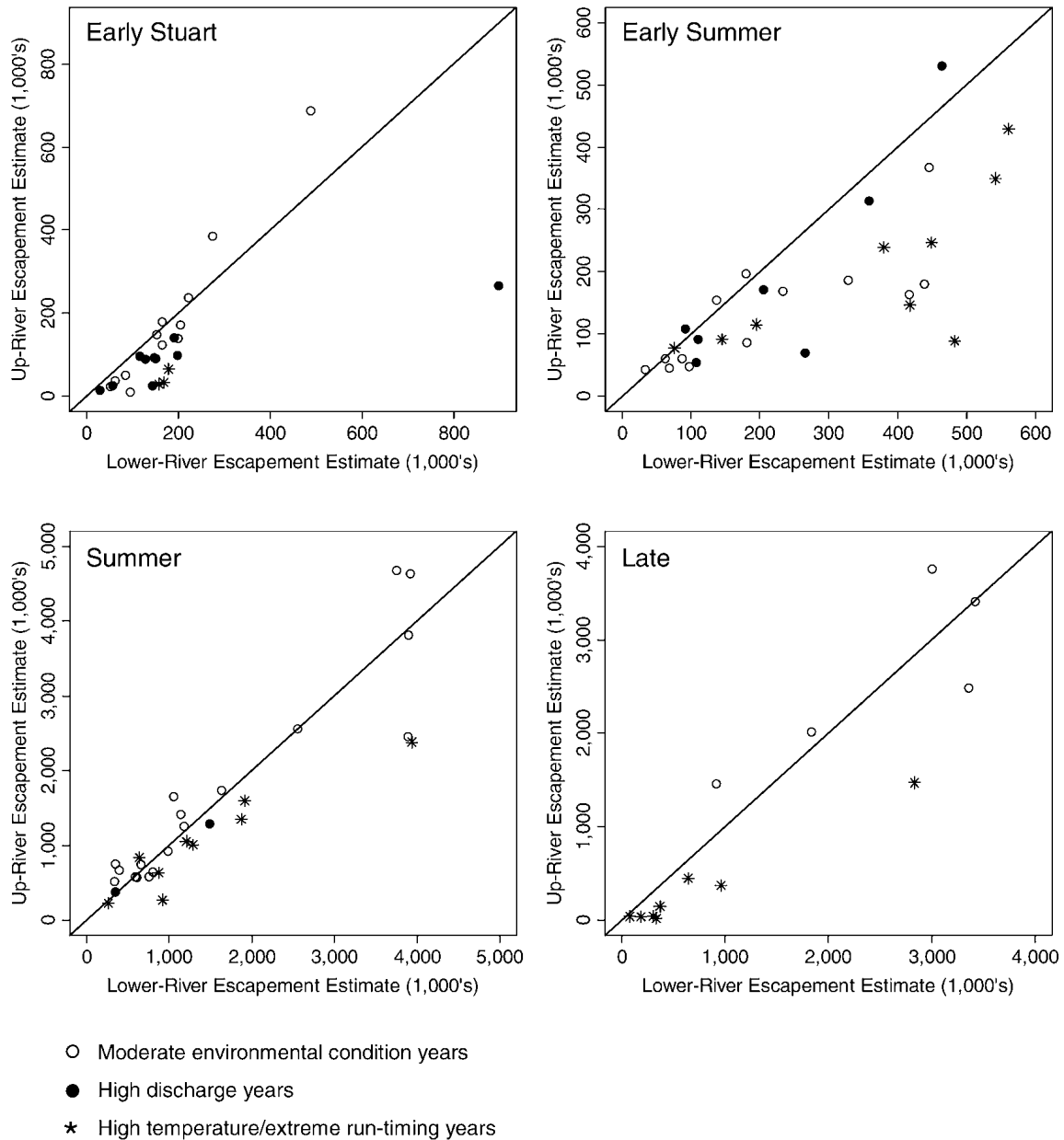


FIGURE 2.—Comparison of lower-river potential spawning escapement (calculated as the Mission escapement estimate – upriver catch) and upriver spawning escapement for each of four Fraser River sockeye salmon run timing groups. High-temperature years are indicated with stars for the early Stuart, early summer, and summer runs. Early run timing years for the late run are also indicated with stars. High-discharge years are indicated with solid circles. Years of moderate environmental or river entry timing conditions are indicated with open circles. A 1:1 line is indicated in solid black. Points falling below the 1:1 line designate years of measured in-river escapement discrepancies.

1985) and Department of Fisheries and Oceans Canada (DFO) databases (Salmon Escapement Database System [NuSEDS]; 1986–2006). Spawning escapement estimates were obtained through a variety of survey methods, including aerial or ground visual surveys, enumeration fences, and mark–recapture techniques.

These methods have been calibrated to adjust for different fish densities and river conditions based on over 70 years of experience in estimating spawning sockeye salmon abundance in the Fraser River (Schubert 2007).

Hell's Gate (Figure 1) was chosen as a geographic

TABLE 1.—Initial set of predictor variables considered for the development of descriptive management adjustment models for each major Fraser River sockeye salmon run timing group.

Variable	Description	Justification	References
\bar{T}	Mean temperature (°C) over a 31-d period surrounding the date by which 50% of the run passed Hell's Gate.	Temperature affects swimming ability and susceptibility to disease, stress, heat shock.	Macdonald et al. (2000); Naughton et al. (2005); Keefer et al. (2008a); Crossin et al. (2008).
T_{\max}	Maximum temperature observed in this 31-d period	As above	
T_{thresh}	Number of days above a given temperature threshold during this 31-d period. Threshold was 18.5°C for early Stuart, 19.5°C for early summer and summer, and 17.5°C for late.	Species-specific tolerances are related to average ambient exposures.	Brett (1971); Servizi and Jensen (1977); Lee et al. (2003); Farrell et al. (2008)
\bar{Q}	Mean discharge (m³/s) over a symmetric 31-d period surrounding the date by which 50% of the run passed Hell's Gate	High discharge relates to higher encounter velocities and therefore to increased energy expenditures.	Macdonald (2000); Rand et al. (2006)
Q_{\max}	Maximum discharge observed in this 31-d period	High discharge produces migration barriers and delays arrival on the spawning ground.	Macdonald (2000)
Q_{thresh}	Number of days above a given discharge threshold (m³/s) during this 31-d period. Threshold was 8,500 m³/s for early Stuart and 6,000 m³/s for early summer. No discharge thresholds were used for summer or late.	Species-specific tolerances are related to average ambient exposures and hydrologic barriers.	
R	The number of days before (or after) the mean 50% run timing date at Mission	Changes in river entry timing result in changes to river environmental exposure.	Cooke et al. (2004); Wagner et al. (2005); Young et al. (2006); Crossin et al. (2008)
N	The mean total abundance of all sockeye salmon in the river during the 31-d period	Density-dependent effects may force fish into parts of the river with suboptimal encounter velocities.	Macdonald (2000)

reference point on which to center the impact of environmental conditions because (1) it is a well-known impediment to salmon migration (Roos 1991; Macdonald et al. 2000) and (2) its environmental conditions can be described accurately using temperature and discharge data collected from nearby Fraser River stations at Qualark Creek and Hope, respectively. Daily discharge values were accessed from the Environment Canada Water Survey of Canada online database (Environment Canada 2006), and daily mean Fraser River water temperatures were from Patterson et al. (2007b).

Biological rationale for predictor variables.—In the absence of a direct measure of natural mortality during the spawning migration, the difference between upriver SE and lower-river PSE estimates (i.e., the escapement discrepancy estimate) is expressed as $\log_e(\text{SE/PSE})$ and provides a measure of the response of each run timing group to environmental conditions during migration (Appendix 1; Hague and Patterson 2007). There is currently no means of estimating and allocating the errors among these escapement estimates or the in-river catch estimates that merge as a component of the discrepancy estimate. The log transformation was required to meet the assumptions of homoscedasticity (Zar 1996) and to constrain predictions in the range 0 or higher. The initial selection of candidate predictor variables (Table 1) was based on a priori knowledge of the mechanistic relationship between temperature,

discharge, river entry timing, fish abundance, and fish migratory biology (described in detail below). A subset of those variables was then selected using statistical methods for assessing model fit.

The effect of temperature on migration success consists of a combination of linear (Crossin et al. 2008) and nonlinear (Farrell et al. 2008) responses. For example, swimming performance increases at a linear rate at low temperature ranges, plateaus within some optimal range, and then rapidly declines at high temperatures (Brett 1971; Lee et al. 2003; Farrell et al. 2008). In addition, continued exposure to high temperatures can elicit a variety of stress responses (Macdonald et al. 2000), leading to immunosuppression and disease development (Anderson 1990; Schreck et al. 2001) or susceptibility to parasitic infection (Servizi and Jensen 1977; St-Hilaire et al. 2002; Wagner et al. 2005; Crossin et al. 2008). Extreme high temperatures can also lead directly to thermal shock and mortality (Servizi and Jensen 1977). Thermal sensitivity appears to be both species- and population-specific and is likely a function of adaptation to ambient temperatures (Lee et al. 2003; Farrell et al. 2008). A parabolic model describing the effect of temperature on optimal swimming performance (Lee et al. 2003) and swim speed (Salinger and Anderson 2006) provided a mechanistic basis for the inclusion of quadratic temperature terms in the MA models. Population-specific sensitivity to thermal shock (Servi-

zi and Jensen 1977; reviewed by Richter and Kolmes 2005), swimming performance (Lee et al. 2003; Farrell et al. 2008), and migration behavior (Hodgson and Quinn 2002; Hyatt et al. 2003; Keefer et al. 2008b) also justified consideration of threshold temperatures specific to each run timing group.

Increases in mean discharge levels constrained within the banks of the Fraser River are associated with increases in river velocities that force fish to swim against higher currents and expend more energy (Hinch and Rand 1998). Consequently, the fish suffer reduced swimming performance (Quinn et al. 1997; Hinch and Rand 2000) and decreased survival (Rand et al. 2006). We also considered high discharge thresholds that can act directly by creating an absolute barrier to upstream migration (Macdonald 2000) and indirectly by restricting fish passage through a reduction in the cross-sectional area of the river that is below critical velocity barriers (Hughes 2004). The effects on survival of discharge and temperature are often difficult to discriminate in field studies (Quinn et al. 1997; Naughton et al. 2005) due to the inverse correlation between these two variables (Patterson and Hague 2007). For example, large escapement discrepancies arise (1) in years with extreme high discharge and associated cool temperatures due to hydraulic migration barriers (Macdonald et al. 2000) and (2) in years with below-average discharge due to the associated extreme high temperatures (Macdonald et al. 2000; Patterson et al. 2007b). We included a quadratic discharge term in the MA models to account for the correlation between discharge and water temperature.

We included a river entry timing variable in the MA models due to the observed correlations between entry time and escapement discrepancies, particularly for the late run timing group. In 1995, late-run fish displayed a behavioral shift to earlier river entry and longer freshwater residency (Cooke et al. 2004; English et al. 2005). The corresponding increase in mortality during the spawning migration has been attributed to (1) exposure to an increase in discharge and warmer temperatures (Figure 3) and (2) an increased duration of freshwater residence (Wagner et al. 2005; Young et al. 2006; Crossin et al. 2008).

Finally, we considered an abundance term to account for anecdotal reports of restricted river passage during years when high discharge coincided with high fish abundance (Macdonald 2000). Increasing velocity and wave drag (Hughes 2004) may limit the availability of optimal migration habitat, creating a density-dependent bottleneck to fish passage. This could either force migrating fish into suboptimal sections of the river (i.e., higher river velocities and increased energy expenditures) or delay migration, thus exposing fish to a longer

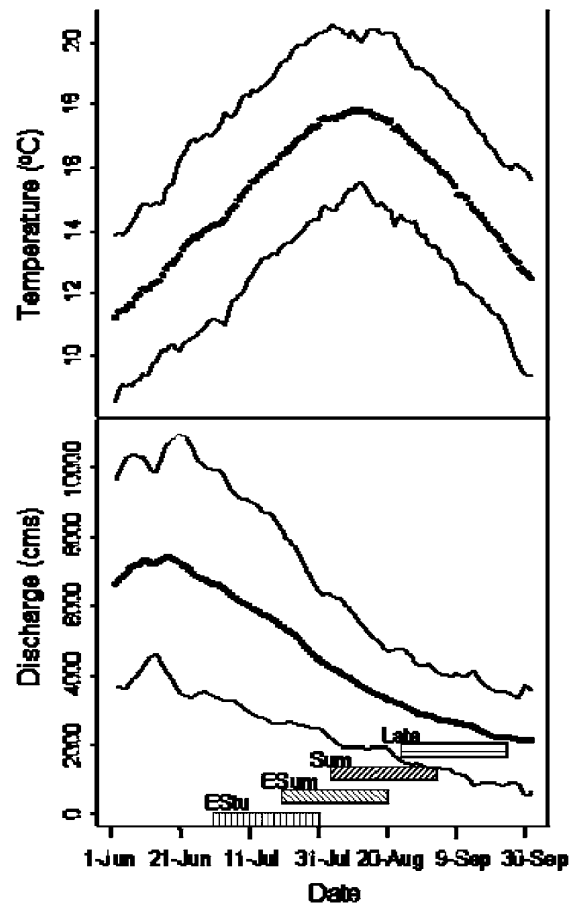


FIGURE 3.—Mean (± 2 SD) temperature ($^{\circ}\text{C}$) and discharge (m^3/s) in the lower Fraser River, June–September 1950–2006. Boxes indicate the symmetric 31-d period around the median Hell’s Gate 50% run timing date for each sockeye salmon run timing group (early Stuart [EStu], early summer [ESum], summer [Sum], and late runs). Temperature is for the Fraser River near Qualark, British Columbia (Patterson et al. 2007a). Discharge is for the Fraser River near Hope (Environment Canada 2006).

freshwater residency and potentially higher temperatures.

Descriptive management adjustment model variables.—Predictive variables for the descriptive MA models were defined using criteria consistent with the observed exposure of sockeye salmon run timing groups to conditions in the lower Fraser River. On average, a 31-d period centered on the Hell’s Gate 50% date (i.e., the date by which 50% of the run has passed Hell’s Gate) captures 90% or more of a run’s exposure to environmental conditions at Hell’s Gate (Hague and Patterson 2007). Therefore, lower-river environmental conditions for each run timing group were expressed in one of three ways: (1) as the mean of the average daily temperature or discharge over a 31-d period centered

TABLE 2.—Initial set of predictor variables considered for development of in-season predictive management adjustment models for each major Fraser River sockeye salmon run timing group given current management and forecasting limitations.

Variable	Description
\bar{T}	Mean temperature (°C) over a 19-d asymmetric ^a period surrounding the date by which 50% of the run passed Hell's Gate
\bar{Q}	Mean discharge (m ³ /s) over a 19-d asymmetric period surrounding the date by which 50% of the run passed Hell's Gate
R	The number of days before (or after) the mean 50% run timing date at Mission

^a 15 d before and 3 d after the 50% date.

on the 50% date, (2) as the maximum average daily temperature or discharge observed during the 31-d period, or (3) as the number of days within the 31-d period when daily average temperature or discharge thresholds were exceeded. Thresholds were set at the high extremes of the ambient conditions experienced by each run timing group, defined as the 95th percentiles of the temperature and discharge distributions for the 31-d period surrounding the median Hell's Gate 50% date (early Stuart group median date = July 14, early summer group = August 11, summer group = August 19, late group = September 9; Figure 3). The temperature thresholds are consistent with the theory that optimal swimming temperatures are closely related to ambient temperatures and that large deviations from historic experience result in reduced survival (Farrell et al. 2008). The river entry timing variable was expressed as the annual anomaly between the 50% date at the Mission hydroacoustic facility and the long-term mean. Finally, the abundance variable was defined as the mean of the daily total sockeye salmon abundance over the 31-d period. Accordingly, eight types of variables were considered as possible predictors of the annual discrepancies between potential escapements estimated at Mission and escapements estimated on the spawning grounds (Table 1).

Prior to model selection, statistical validation for the variables in the descriptive MA model was assessed using regression analysis. Strong correlations (Pearson's product-moment correlation coefficient $r > 0.70$) were identified among several of the predictor variables in Table 1. Given the potential for multicollinearity bias, statistical significance of environmental and run timing variables in the current MA models was tested using a multiple regression of principal component (PC) scores (e.g., Naughton et al. 2005). Principal components were first derived from correlation matrices of the predictor variables. A subset of components was then selected using the broken stick criterion (King

and Jackson 1999; McGarigal et al. 2000). For each run timing group, we tested our hypothesis of a significant relationship between the environmental variables in Table 1 and the escapement discrepancies by regressing the retained component scores on the MA response variable, $\log_e(\text{SE/PSE})$ (Naughton et al. 2005).

Predictive management adjustment model variables.—A modified set of variables was evaluated for use in predictive MA models suitable for forecasting escapement discrepancies during in-season management of Fraser River sockeye salmon (Table 2). Current management and forecasting constraints prohibit the use of some of the biologically relevant variables used in the descriptive MA models. First, the exposure time frame in the lower Fraser River was constrained to 15 d before and 3 d after the Hell's Gate 50% date although, on average, this 19-d period captures less than 75% of a run (Hague and Patterson 2007). The shortened time frame is required for in-season models because run timing forecasts cannot be updated until the majority of each run passes through marine test fisheries off the west coast of Vancouver Island and in Johnstone Strait (Figure 1); this does not occur until approximately 10 d prior to the Hell's Gate 50% date for the early and summer runs. Additionally, in-season predictions of escapement discrepancies depend on forecasted environmental values from hydrologic models for the Fraser River. Similar to weather forecasting models, there is a continual reduction in the accuracy of river temperature and discharge forecasts with time (Foreman and Morrison 2005). Currently, river conditions can only be reliably predicted for a 9-d period, and a combination of 10 d of observed lower Fraser River temperature and discharge and 9 d of forecasted temperature and discharge are used to provide the 19 d of environmental data used in the predictive MA models (Morrison 2005). Furthermore, the individual daily environmental forecasts generated by current in-season environmental models are uncertain (Morrison 2005); therefore, reliable predictions of threshold and maximum temperature and discharge variables are not presently feasible. Finally, abundance variables were omitted from the predictive MA models because daily run size forecasts are difficult to predict until fish have migrated past the Mission hydroacoustic facility.

Model selection criteria.—The AIC corrected for small sample size (AIC_c ; Burnham and Anderson 2002) was computed for a range of descriptive and predictive MA models. Given the large number of correlated variables, three suites of descriptive models were evaluated for each run timing group by using threshold, mean, and maximum environmental variables, respectively. The AIC_c values were transformed

into AIC_c weights (w) and AIC_c differences (ΔAIC_c ; Burnham and Anderson 2002) in order to assess the fit of each MA model i relative to all other models evaluated. As a rule of thumb, models with ΔAIC_c less than 2 in comparison with the “best-fit” model (i.e., the model with the lowest AIC_c value) are well supported (Burnham and Anderson 2002).

All statistical procedures for the principal components analysis, regressions, and AIC_c were performed using R statistical software (version 2.8.0).

Results

Consistent with our knowledge of the mechanistic relationships between spawning migration mortality and freshwater environmental conditions, the regression analysis identified statistically significant relationships between PC scores related to environmental variables (Table 3) and escapement discrepancies (Table 4). The variables associated with the three PC axes describing the majority of the variability in the environmental data set varied across run timing groups (Table 3), as did the variables associated with the significant component scores in the multiple regressions (Table 4). This result further validates the use of variables specific to each run timing group during the current application of MA models.

Various combinations of river temperature and discharge variables influenced escapement discrepancies in the three earliest-timed groups. Temperature and discharge thresholds of 18.5°C ($T_{18.5}$) and 8,500 m³/s ($Q_{8.5}$) described the variability in early Stuart run escapement discrepancies (reflected in Table 4 by the regression of PC3 scores on escapement discrepancies; $P = 0.03$). Mean and maximum temperature and discharge variables (\bar{T} , T_{\max} , \bar{Q} , and Q_{\max} ; Table 3) were associated with the early summer-run and summer-run escapements (reflected by the significance of the regression of PC1 scores on their escapement discrepancies; $P = 0.05$ and 0.02, respectively). Not surprisingly, the dramatic shift in late-run river entry behavior in 1995 resulted in run timing explaining the majority of the variability in the environmental data for this group (Table 3). Run timing and river discharge were both associated with significant PCs (PC1: $P < 0.002$; PC2: $P = 0.05$) for the late-run regression.

The application of AIC_c selection criteria reduced the total number of candidate descriptive MA models from 140 to 13 (models with $\Delta AIC_c < 2$) and identified consistent differences among the types of predictor variables associated with the best-fit MA models for each run timing group (Table 5). Best-fit model variables were generally comparable with those variables deemed significant after the multiple regression of the PC scores (Table 4 versus Table 5).

TABLE 3.—Principal component (PC) loadings for first three axes and summary statistics performed for the predictor variables provided in Table 1 during the migration period for each Fraser River sockeye salmon run timing group (1977–2006). The maximal loadings on each retained component are in bold; C represents communalities (i.e., the percentage of variance in each variable explained by the three retained components). See Table 1 for full description of variables ($Q_{8.5}$ is Q_{thresh} at a discharge of 8,500 m³/s; Q_6 is Q_{thresh} at a discharge of 6,000 m³/s).

Variable	PC1	PC2	PC3	C
Early Stuart				
$Q_{8.5}$	−0.660	−0.170	0.597	0.821
\bar{Q}	− 0.915	−0.127	0.257	0.920
Q_{\max}	− 0.858	−0.252	0.189	0.834
$T_{18.5}$	0.787	−0.091	0.532	0.911
\bar{T}	0.932	−0.215	0.108	0.928
T_{\max}	0.898	−0.070	0.273	0.887
R	0.211	− 0.876	−0.012	0.812
N	−0.091	− 0.837	−0.313	0.808
Eigenvalue	4.358	1.637	0.927	
Percent variance	54.5	20.4	11.6	
Cumulative percent	54.5	74.9	86.5	
Early summer				
Q_6	−0.757	0.303	−0.421	0.824
\bar{Q}	− 0.866	0.381	−0.222	0.946
Q_{\max}	− 0.878	0.310	−0.270	0.940
$T_{19.5}$	0.733	0.550	−0.306	0.934
\bar{T}	0.822	0.520	−0.026	0.948
T_{\max}	0.790	0.524	−0.169	0.927
R	0.414	− 0.710	−0.345	0.795
N	0.287	−0.409	− 0.789	0.872
Eigenvalue	4.187	1.853	1.164	
Percent variance	52.3	23.2	14.6	
Cumulative percent	52.3	75.5	90.0	
Summer				
\bar{Q}	− 0.769	−0.445	0.431	0.975
Q_{\max}	− 0.768	−0.415	0.470	0.982
$T_{19.5}$	0.716	−0.543	0.138	0.827
\bar{T}	0.757	−0.551	0.017	0.877
T_{\max}	0.798	−0.491	0.171	0.908
R	0.392	0.779	0.309	0.856
N	0.488	0.475	0.662	0.902
Eigenvalue	3.295	2.042	0.989	
Percent variance	47.1	29.2	14.1	4.48
Cumulative percent	47.1	76.2	90.4	94.9
Late				
\bar{Q}	−0.589	0.793	0.057	0.979
Q_{\max}	−0.514	0.828	0.112	0.963
$T_{17.5}$	−0.875	−0.304	0.055	0.861
\bar{T}	−0.837	−0.482	−0.077	0.939
T_{\max}	−0.877	−0.379	0.121	0.928
R	0.969	−0.081	−0.066	0.950
N	0.255	−0.123	0.968	1.000
Eigenvalue	3.85	1.81	0.962	
Percent of variance	55.0	25.8	13.7	
Cumulative percent	55.0	80.8	94.6	

Temperature and discharge thresholds as well as fish abundance variables provided the best fit to early Stuart data. Models with mean temperature and discharge best described the variability in early summer-run discrepancies, and summer-run discrepancies were best fit using mean temperature variables alone. In contrast to

TABLE 4.—Tests of significance of the three principal component (PC) variables using PC scores as observations are provided as a valid statistical test of the ability of environmental, river entry timing, and run size variables to predict differences between upriver spawning escapement (SE) and lower-river potential spawning escapement (PSE) estimates ($\log_e[\text{SE}/\text{PSE}]$) for Fraser River sockeye salmon. The number of years used to predict $\log_e[\text{SE}/\text{PSE}]$ in each run was primarily determined by the operation of the Mission hydroacoustic facility; P -values followed by an asterisk are significant ($\alpha = 0.10$).

Run	Years	Overall P	R^2	P -value for:				
				PC1	PC1 ²	PC2	PC2 ²	PC3
Early Stuart	24	0.002	46	0.78	0.92	0.08*		0.03
Early summer	28	0.03	24	0.06*	0.05	0.46		0.80
Summer	28	0.003	38	0.06*	0.02	0.90		0.83
Late	14	0.003	72	0.002		0.05	0.52	0.67

TABLE 5.—Descriptive management adjustment model selection for each Fraser River sockeye salmon run timing group. A full suite of models using the descriptive variables listed in Table 1 was evaluated and grouped by threshold, mean, and maximum environmental values. Adjusted R^2 values, corrected Akaike's information criterion difference (ΔAIC_c) values, and relative AIC_c weights (w) are presented for each model. The results for the best-fit models are in bold.

Model	Early Stuart			Early summer			Summer			Late		
	R^2	ΔAIC_c	w	R^2	ΔAIC_c	w	R^2	ΔAIC_c	w	R^2	ΔAIC_c	w
$T_{\text{thresh}} + Q_{\text{thresh}} + R + N$	53	0.59	0.19	16	6.93	0.01						
$T_{\text{thresh}} + Q_{\text{thresh}} + R$	49	2.06	0.09	19	5.85	0.01						
$T_{\text{thresh}} + Q_{\text{thresh}} + N$	54	0.00	0.25	15	7.17	0.01						
$T_{\text{thresh}} + R + N$	26	11.9	0	11	8.43	0	37	9.87	0	79	13.9	0
$Q_{\text{thresh}} + R + N$	6	18.0	0	0	13.0	0						
$T_{\text{thresh}} + R$	24	12.9	0	14	7.70	0.01	39	9.40	0	81	11.6	0
$T_{\text{thresh}} + N$	29	11.1	0	14	7.97	0.01	40	9.07	0	22	31.2	0
$Q_{\text{thresh}} + R$	9	17.4	0	0	12.7	0						
$Q_{\text{thresh}} + N$	10	17.1	0	0	12.4	0						
$T_{\text{thresh}} + Q_{\text{thresh}}$	51	1.66	0.11	16	7.07	0.01						
T_{thresh}	27	12.3	0	15	7.96	0.01	40	9.38	0	28	30.1	0
Q_{thresh}	11	17.3	0	0	13.3	0						
$\bar{T} + \bar{T}^2 + \bar{Q} + \bar{Q}^2 + R + N$	38	8.92	0	25	4.04	0.03	51	3.40	0.04	87	18.3	0
$\bar{T} + \bar{T}^2 + \bar{Q} + \bar{Q}^2 + R$	40	7.31	0.01	24	1.36	0.13	53	1.69	0.09	88	8.34	0.01
$\bar{T} + \bar{T}^2 + \bar{Q} + \bar{Q}^2 + N$	42	6.72	0.01	29	2.32	0.08	52	2.33	0.06	82	16.9	0
$\bar{T} + \bar{T}^2 + R + N$	29	11.3	0	12	7.95	0.01	53	1.34	0.10	75	18.5	0
$\bar{Q} + \bar{Q}^2 + R + N$	0	19.9	0	16	6.93	0.01	0	23.3	0	89	6.52	0.03
$\bar{T} + \bar{T}^2 + R$	30	10.5	0	16	4.02	0.03	55	0.24	0.18	76	13.3	0
$\bar{T} + \bar{T}^2 + N$	32	9.98	0	15	7.32	0.01	54	0.57	0.15	14	33.8	0
$\bar{Q} + \bar{Q}^2 + R$	3	18.7	0	12	5.64	0.02	0	23.8	0	90	0	0.89
$\bar{Q} + \bar{Q}^2 + N$	4	18.6	0	17	6.54	0.01	0	23.5	0	71	18.4	0
$\bar{T} + \bar{T}^2 + \bar{Q} + \bar{Q}^2$	42	5.96	0.01	27	0	0.26	53	1.25	0.11	85	8.81	0.01
$\bar{T} + \bar{T}^2$	31	10.3	0	17	4.01	0.03	56	0	0.20	21	30.3	0
$\bar{Q} + \bar{Q}^2$	6	18.0	0	14	5.24	0.02	0	23.2	0	74	13.9	0
$R + N$	0	20.9	0	0	12.7	0	0	24.1	0	75	15.5	0
R	0	20.6	0	0	12.2	0	0	2.50	0	76	12.4	0
N	0	20.2	0	0	10.3	0	1	23.7	0	0	35.3	0
$T_{\text{max}} + T_{\text{max}}^2 + Q_{\text{max}} + Q_{\text{max}}^2 + R + N$	50	3.64	0.04	25	4.09	0.03	44	7.16	0.01	84	20.3	0
$T_{\text{max}} + T_{\text{max}}^2 + Q_{\text{max}} + Q_{\text{max}}^2 + R$	48	4.01	0.03	28	2.63	0.07	46	5.43	0.01	86	13.2	0
$T_{\text{max}} + T_{\text{max}}^2 + Q_{\text{max}} + Q_{\text{max}}^2 + N$	52	1.72	0.11	28	2.78	0.06	46	5.44	0.01	72	23.5	0
$T_{\text{max}} + T_{\text{max}}^2 + R + N$	44	5.37	0.02	15	6.98	0.01	42	7.37	0.01	78	17.0	0
$Q_{\text{max}} + Q_{\text{max}}^2 + R + N$	0	20.5	0	11	8.44	0	5	21.7	0	87	9.61	0.01
$T_{\text{max}} + T_{\text{max}}^2 + R$	42	6.04	0.01	16	4.02	0.03	44	6.30	0.01	80	13.6	0
$T_{\text{max}} + T_{\text{max}}^2 + N$	46	4.03	0.03	19	5.88	0.01	43	6.90	0.01	18	33.2	0
$Q_{\text{max}} + Q_{\text{max}}^2 + R$	0	19.4	0	12	5.64	0.02	3	22.5	0	88	6.58	0.03
$Q_{\text{max}} + Q_{\text{max}}^2 + N$	1	19.2	0	17	6.54	0.01	3	22.5	0	43	28.0	0
$T_{\text{max}} + T_{\text{max}}^2 + Q_{\text{max}} + Q_{\text{max}}^2$	50	2.43	0.07	16	6.95	0.01	48	4.06	0.03	73	19.5	0
$T_{\text{max}} + T_{\text{max}}^2$	43	5.71	0.01	17	4.01	0.03	45	6.35	0.01	24	31.2	0
$Q_{\text{max}} + Q_{\text{max}}^2$	4	18.6	0	14	5.24	0.02	5	22.2	0	46	26.4	0

TABLE 6.—Predictive management adjustment (MA) model selection for each Fraser River sockeye salmon run timing group. A full suite of models using the descriptive variables listed in Table 1 was evaluated and grouped by threshold, mean, and maximum environmental values. Adjusted R^2 values, corrected Akaike's information criterion difference (ΔAIC_c) values, and relative AIC_c weights (w) are presented for each model. The results for the best-fit models are in bold. The currently applied MA models (Appendix 1) are in italics.

Model	Early Stuart			Early summer			Summer			Late		
	R^2	ΔAIC_c	w	R^2	ΔAIC_c	w	R^2	ΔAIC_c	w	R^2	ΔAIC_c	w
$\bar{T} + \bar{T}^2 + \bar{Q} + \bar{Q}^2 + R$	9	2.20	0.09	13	1.33	0.23	35	2.00	0.13	88	4.77	0.07
$\bar{T} + \bar{T}^2 + R$	14	0.12	0.27	4	4.11	0.06	38	0.35	0.29	71	13.1	0
$\bar{Q} + \bar{Q}^2 + R$	3	3.33	0.05	7	3.27	0.09	0	15.3	0	88	0	0.79
$\bar{T} + \bar{T}^2 + \bar{Q} + \bar{Q}^2$	<i>13</i>	<i>0.65</i>	<i>0.20</i>	<i>17</i>	<i>0</i>	<i>0.44</i>	<i>37</i>	<i>0.84</i>	<i>0.23</i>	86	3.69	0.13
$\bar{T} + \bar{T}^2$	15	0	0.28	6	3.92	0.06	40	0	0.35	25	26.4	0
$\bar{Q} + \bar{Q}^2$	6	2.55	0.08	10	2.67	0.12	0	14.6	0	73	11.3	0
R	0	5.08	0.02	0	6.51	0.02	0	16.1	0	76	9.20	0.01

the earlier run timing groups, variance in late-run discrepancies was poorly described by river temperature and was best fit using mean discharge and timing of river entry. Relative values of w were evenly distributed among early Stuart, early summer, and summer descriptive MA models (20–26% of w assigned to the best-fit model). Although these low percentages reduce our confidence that a single “best” MA model exists for each early run timing group, the models comprising the majority of the total w for each of the early run timing groups (models with $\Delta AIC_c < 2$) were similar in structure (i.e., similar environment variables) to the best-fit model. In contrast, a w -value of almost 90% was associated with the best-fit late-run model, giving greater confidence in the ability of a single model to describe escapement discrepancies than arose during the selection of MA models for the other run timing groups (Table 5).

In most cases, the structure of predictive MA models and that of descriptive MA models were identical, but the in-season constraints placed on the selection of variables for the predictive MA models (e.g., 19-d means, absence of threshold and maximum environmental variables) often resulted in reductions in model fit (larger AIC_c ; Table 5 versus Table 6). The values of ΔAIC_c between the best-fit descriptive model and the best-fit predictive model were more substantial for the early Stuart run ($\Delta AIC_c = 15.6$) and summer run (9.43) than for the early summer run (3.68) and late run (3.39). The large ΔAIC_c for the early Stuart predictive model corresponds to the shift in model structure from a threshold-based descriptive MA model (Table 5) to a mean temperature predictive MA model (Table 6).

Discussion

Mortality during the sockeye salmon spawning migration is influenced by a combination of several environmental factors. This paper quantifies escapement discrepancies as a function of environmental

variation and supports independent observations that large numbers of Fraser River sockeye salmon die during the freshwater portion of their migration in years with extreme river temperature (Macdonald et al. 2000; Patterson et al. 2007b; Crossin et al. 2008; Farrell et al. 2008), high river discharge (Hinch and Rand 1998; Macdonald 2000), and early river entry (Cooke et al. 2004; Crossin et al. 2008). Moreover, the differences in MA model structure among major run timing groups can be ascribed to differences in their freshwater environmental exposure (Hague et al. 2008) and potentially to stock-specific behavioral and physiological adaptations that have evolved to deal with natural variability in conditions during spawning migrations (Hodgson and Quinn 2002; Crossin et al. 2004; Farrell et al. 2008). Consequently, the development and evaluation of the structure of MA models may—in addition to informing fisheries management actions—provide insight into how environmental conditions can act as strong selective forces on each run timing group.

Estimates of high spawning migration mortality among early Stuart sockeye salmon in years with extreme discharge are consistent with the exposure of this group to the highest discharge levels of any run timing group at threshold levels known to impede fish passage in the lower Fraser River (i.e., $>8,000 \text{ m}^3/\text{s}$; Macdonald 2000). Interestingly, the 18.5°C temperature threshold for the early Stuart run is well below temperatures associated with acute thermal stress (e.g., 21°C ; Servizi and Jensen 1977). However, it is likely that the 18.5°C threshold value is a proxy for the more severe temperature exposures (i.e., $>21^\circ\text{C}$) these fish encounter upstream in the Stuart Lake–Nechako River system during warm summers (Macdonald et al. 2007; Hague et al. 2008). The cumulative impact of temperatures above 18.5°C in the lower reaches and above 20°C in upper reaches of the Fraser River is likely lethal for many fish in a group that migrates over

1,000 km in less than 1 month (Macdonald et al. 2000). The rationale for modeling an abundance term originated from speculation that density-dependent bottlenecks exist in difficult canyon sections. Therefore, it is more difficult to interpret the selection of a fish density variable for the early Stuart run but not for the other three run timing groups, which are considerably more abundant. However, early Stuart models excluding the abundance term performed similarly to the best-fit MA model ($\Delta AIC_c < 2$), suggesting that more analyses are needed to interpret the importance of fish density in relation to migration mortality for Fraser River sockeye salmon.

Estimates of high spawning migration mortality among early summer-run and summer-run sockeye salmon in years with high water temperatures are consistent with their migration timing during the warmest period of the year. While these temperatures rarely exceed lethal thresholds, chronic exposure to sublethal temperatures that deviate substantially from thermal optima can still compromise migratory success (Wagner et al. 2005; Crossin et al. 2008; Farrell et al. 2008). The early summer-run fish are in the river before the summer-run fish and may also be periodically exposed to high-flow events (Patterson and Hague 2007) that are unlikely to reach extreme thresholds but will necessitate increased energy expenditures that can compromise migration success (Rand et al. 2006).

Estimates of high spawning migration mortality among late-run sockeye salmon in years of early river entry timing and high discharge are consistent with observations (Cooke et al. 2004) and fish energetics research (Rand et al. 2006). However, in contrast to the other run timing groups, temperature was not identified as a significant predictor for the late-run MA model. This is despite the fact the high mortality for late-run fish is attributed to extended freshwater residency in warm water (Cooke et al. 2004; English et al. 2005; Young et al. 2006; Farrell et al. 2008), leading to higher rates of disease development and mortality (St-Hilaire et al. 2002; Wagner et al. 2005; Young et al. 2006; Crossin et al. 2008). One explanation for the deviation between biological and statistical significance of temperature effects on spawning migration mortality of late-run sockeye salmon involves the covariation among river entry timing, discharge, temperature, and freshwater residency variables. Other authors have documented similar difficulties in ascribing aspects of salmon migration biology to a single environmental variable (see Quinn et al. 1997; Naughton et al. 2005; Macdonald et al. 2007). The timing of river entry is likely a more powerful predictor of late-run escapement discrepancies because early

entry timing encapsulates three factors known to increase salmon migration mortality: high discharge, high temperature, and longer freshwater residency. This highlights a potential limitation of interpreting the biological significance of a single variable within multivariate analyses and the importance of continuing to research the mechanistic relationships linking environmental conditions to salmon migration success.

Overall, the choices of discrepancy predictors are consistent with our knowledge of the risk of exposure to environmental conditions and the observed migratory stress response that are specific to each run timing group. This provides a biological rationale for the use of environmental variables in the MA models.

The multiple regression and AIC_c analyses provided empirical support for the use of freshwater environmental variables to predict escapement discrepancies currently used to inform Fraser River sockeye salmon harvest decisions. For example, over 50% of the variation in discrepancies (adjusted R^2) in three of the four run timing groups could be attributed to environmental variation; the early summer run was the exception (maximum adjusted $R^2 = 0.27$). In years of extreme environmental conditions, it is reasonable to ascribe the majority of the in-river escapement discrepancies to environmental conditions; this statement is supported by numerous biological studies (cited herein) and in-river observations (Macdonald 2000; Macdonald et al. 2000). However, in years of moderate environmental conditions, a larger portion of the unexplained variation in discrepancies is likely due to a combination of errors in estimates of lower-river and spawning ground escapement and in-river fishery catches. It is also possible that migration conditions are correlated with estimation errors since high fish densities and fish distribution changes associated with environmental conditions can create a bias in hydro-acoustic estimates of lower-river escapements (Xie et al. 2002). However, previous work has not shown river environmental conditions to bias spawning escapement estimates (Schubert and Houtman 2007), and there is no current information available on possible biases to in-river catch estimates. The larger, unexplained variance in the early summer-run MA model versus models for the other run timing groups could be associated with the large number of early summer populations dispersed throughout the Fraser River watershed, which experience a variety of migratory conditions en route to spawning grounds (Hague et al. 2008). Thermal tolerance among these early summer populations may also vary (Lee et al. 2003; Farrell et al. 2008) and, when combined with large interannual swings in relative abundance, may provide an additional source of unexplained variance. Future research

should explore the structure and magnitude of the errors in lower-river and spawning ground escapement estimates and in-river catch estimates as well as the contributions of individual populations within a group to the total MA. These efforts better quantify unexplained variance and improve our ability to describe escapement discrepancies.

The significance and fit of MA models in our study were established using observed environmental variables, but during the execution of a sockeye salmon fishery the reliability of escapement discrepancy predictions used to inform managers will depend on both the significance of the MA model structure and the reliability of forecasted environmental variables. Management adjustment models with fewer variables, variables that can be forecasted with greater certainty, or both will probably provide the most reliable in-season management advice. Keefer et al. (2008b) found that models using relatively few environmental predictor variables were still effective at describing the variance in river entry timing for Chinook salmon *O. tshawytscha* in the Columbia River. Furthermore, caution should be applied when using the results of the best-fit AIC_c procedures to select predictive MA models that rely on forecasted predictor variables because AIC_c values do not reflect the errors in variables associated with environmental forecasts (Foreman et al. 2001; Morrison and Foreman 2005). Efforts to include forecast uncertainty on long-range environmental forecast models used in preseason planning for the Fraser River sockeye salmon fishery have already occurred and clearly indicate that the models with the best fit do not necessarily produce the most accurate predictions if there is substantial uncertainty introduced by forecasted predictor variables (Patterson and Hague 2007). The integration of environmental forecasting errors into the model selection process, such as that for MA models, is an important area for future research in ecosystem-based management.

We acknowledge that alternative variables, combinations of variables, alternate models, or a combination thereof may provide an improved fit to the escapement discrepancies despite careful attention to the biological rationale behind our choice of predictor variables and model structures. The AIC_c procedure was effective at reducing the total number of candidate MA models (especially for early Stuart, early summer, and late run timing groups), but AIC_c values are specific to the model set explored and may not provide definitive evidence of the “best” model (Link and Barker 2006). In our study, several alternative models with similar values of w were identified among the summer-run descriptive MA models (e.g., six models had $\Delta AIC_c < 2$), suggesting that the existence of a single “best” model is unlikely. One approach to combining models

with similar w -values is to apply model-averaging approaches that can help reduce the bias and improve the precision in predicted values (Burnham and Anderson 2002; Johnson and Omland 2004; Link and Barker 2006).

A next step for assessment of in-season MA models is to test the validity of model predictions using a retrospective, cluster, or leave-one-out analysis (e.g., Haeseker et al. 2005). A simplistic approach to quantifying the benefit of using environmental MA models is to compare the mean absolute error (Haeseker et al. 2005) using the best-fit predictive models versus no MA. A preliminary analysis applying this approach indicates that if the best predictive models were applied to the data set we evaluated, the uncertainty in forecasting spawning escapements would be reduced by thousands of fish for each run timing group (early Stuart group = 69,600; early summer group = 117,100; summer group = 1,162,000; late group = 1,265,250). Reducing uncertainties can ultimately serve to improve the achievement of spawning escapement and harvest objectives (Link and Peterman 1998; Holt and Peterman 2008).

The MA models provide a simple and reliable method of incorporating environmental conditions into in-season predictions of salmon migration success and have already been applied to improve the fisheries management of Fraser River sockeye salmon. The performance of such ecosystem-based models for predicting mortality of sockeye salmon during their spawning migration will improve through a better understanding of salmon migration biology, a continued evaluation of the management models, and improvements in monitoring and forecasting of environmental variables.

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Appendix 1: Current Management Adjustment Models

The development of predictive management adjustment (MA) models has undergone several phases. Prior model selection procedures using adjusted R^2 performance measures resulted in the selection of several models. The most general model structure used for the early Stuart, early summer, and summer run timing groups is equation (A.1), and the model in equation (A.2) is used for the late run timing group:

$$\log_e \left(\frac{SE}{PSE} \right) \sim a + b\bar{T} + c\bar{T}^2 + d\bar{Q} + e\bar{Q}^2, \quad (A.1)$$

$$\log_e \left(\frac{SE}{PSE} \right) \sim a + bR, \quad (A.2)$$

where SE is spawning ground escapement; PSE is lower-river escapement adjusted for catch; \bar{T} is mean river temperature (°C) near Qualark Creek, British Columbia; \bar{Q} is mean river discharge (m³/s/1,000) near Hope, British Columbia; and R is the date by which 50% of the sockeye salmon from a run timing group have passed Hell's Gate, British Columbia.

Environmental means are quantified using the

average of daily mean river temperatures and discharges over an asymmetric 19-d period surrounding the forecasted Hell's Gate 50% date for each run timing group (i.e., 15 d before and 3 d after that date).

The response variable from the MA model is then transformed into absolute numbers using equation (A.3) to calculate the number of additional fish required to pass Mission to achieve the spawning escapement target (SET):

$$MA = SET \times \left(\frac{PSE}{SE} - 1 \right). \quad (A.3)$$

The MA is set to zero in years when it exceeds the number of fish available after the SET is subtracted from the total abundance. The MA is then added to the original SET and the in-river allocations to aboriginal (C_A) and recreational (C_{REC}) catches in order to calculate an adjusted SET (SET_{adj}) as follows:

$$SET_{adj} = SET + MA + C_A + C_{REC}, \quad (A.4)$$

where the SET_{adj} is the total number of fish for each run timing group required to pass Mission to achieve the SET.