

Retrospective patterns of differential mortality and common year-effects experienced by spring and summer chinook salmon (*Oncorhynchus tshawytscha*) of the Columbia River

Richard B. Deriso, David R. Marmorek, and Ian J. Parnell

Abstract: We used spawner–recruit data to estimate the instantaneous differential mortality (μ) experienced by seven Snake River spring and summer chinook (*Oncorhynchus tshawytscha*) stocks relative to six lower Columbia River stocks. We applied 37 Ricker stock–recruit models to these data, incorporating different assumptions about measurement error, transport survival, intrinsic productivity, methods of estimating μ , and common year-effects that affect the survival of all stocks. Estimates of mean μ for the 12 best models ranged from 0.55 to 1.90 (mean of 1.09), implying that passage from Lower Granite Dam to John Day Dam reduced recruitment of 1970–1990 Snake River broods by an average of 42–85% (mean of 66%). Differential mortality was cyclical and moderately high in the 1970s brood years, low for 1980–1983, near average in 1984–1989, and high in 1990. Our empirical estimates of μ showed low bias and were between those produced by two mechanistic passage models. The best empirical models included common year-effects, which shifted from generally positive effects on 1952–1968 brood years to generally negative effects on 1970–1990 broods. Year-effects were not significantly correlated with two climate indices or with water travel time (the time that water takes to travel down the Columbia River).

Résumé : Des données sur les géniteurs et les recrues nous ont permis d'estimer la mortalité différentielle instantanée (μ) chez sept stocks de printemps et d'été du Saumon quinnat dans la rivière Snake, par comparaison à six stocks de l'aval du fleuve Columbia. Nous avons analysé ces données à l'aide de 37 modèles de stock–recrutement de Ricker qui incorporent diverses présuppositions concernant les erreurs de mesure, la survie au transport, la productivité intrinsèque, les méthodes d'estimation de μ et les effets généraux de l'année sur la survie de tous ces stocks. Les estimations de μ pour les 12 meilleurs modèles variaient de 0,55 à 1,90 (moyenne de 1,09), ce qui indique que le passage du barrage Lower Granite à celui de John Day a réduit les cohortes de 1970–1990 de la rivière Snake d'en moyenne 42–85 % (moyenne globale de 66 %). La valeur de μ a varié de façon cyclique, modérément élevée chez les cohortes des années 1970, faible chez celles de 1980–1983, près de la normale chez celles de 1984–1989 et élevée chez celle de 1990. Nos estimés empiriques de μ montrent peu d'erreur et se situent entre ceux générés par deux modèles mécanistes de passage des poissons. Les meilleurs modèles empiriques incorporent les effets généraux de l'année, qui ont varié de généralement favorables pour les cohortes de 1952–1968 à généralement négatifs pour les cohortes de 1970–1990. Les effets de l'année ne sont pas en corrélation significative avec les deux indices climatiques, ni avec le temps requis par l'eau pour descendre le Columbia.

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Introduction

Snake River spring and summer chinook salmon (*Oncorhynchus tshawytscha*) stocks have declined dramatically since the mid-1970s. They were listed as threatened under the Endangered Species Act in 1992 and reclassified as endangered in August 1994 on an emergency basis. The mid-

1970s was a period of major changes in the anthropogenic and environmental conditions encountered by these stocks. The last of the Snake River dams were completed, hatchery production increased dramatically, there was a large increase in the number of fish transported in barges around the hydropower system, and there was a major shift in ocean conditions in the Northeast Pacific. Because all of these changes occurred around the same time, there are many hypotheses about the relative importance of these factors on the mortality of Snake River chinook salmon. These hypotheses were embodied in different management models, which had different underlying assumptions and consequently provided conflicting advice to managers about current and future actions that might best recover listed chinook stocks.

One of the key issues has been the magnitude and causes of systematic differences in spawner-to-recruit survival rates between spring and summer chinook stocks originating in Snake River sub-basins and stocks originating in sub-basins

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R.B. Deriso. Inter-American Tropical Tuna Commission,
Scripps Institute of Oceanography, La Jolla, CA 92093-0203,
U.S.A.

D.R. Marmorek and I.J. Parnell.¹ ESSA Technologies Ltd.,
300–1765 W. 8th Avenue, Vancouver, BC V6J 5C6, Canada.

¹Corresponding author (e-mail: iparnell@essa.com).

further downstream in the Columbia River system, as found in Schaller et al. (1999) (i.e., differences that remain after accounting for different productivity of stocks and for random effects in individual streams). We call these systematic differences "differential mortality". Because lower-river stocks pass through or around fewer dams, are not transported, have fewer hatchery influences, and possibly inhabit different areas of the Pacific Ocean than Snake River stocks, any of these factors could be explanations for observed differences in survival.

In an effort to resolve debates over this and other issues, the Plan for Analyzing and Testing Hypotheses (PATH) was initiated in 1995 (see Marmorek and Peters (2001) for a description of the PATH process). Within the PATH framework, agency and independent scientists rigorously evaluated evidence for and against explicit hypotheses about the distribution, cause, and magnitude of mortality over the life cycle of spring chinook salmon. They developed new data and analytical methods to address old questions. In particular, reconstructed time series of spawner and recruit data for spring chinook stocks of the Columbia River provided the opportunity to explore hypotheses about spatial and temporal patterns in mortality (Marmorek et al. 1998). Stock and recruitment data can provide a powerful basis for inferential hypothesis testing and parameter estimation regarding mortality experienced by juvenile chinook salmon during their down-river migration.

In this paper, we describe an analysis that takes advantage of this rich data set to explore retrospective patterns in the differential mortality experienced by chinook salmon populations from different regions of the Columbia River basin. Our goal was to estimate differential mortality by fitting stock and recruitment models to available data on recruitment and escapement and ancillary information. We exploit the fact that many of the dams along the Columbia and Snake rivers were completed at various times encompassed by the time series of available stock and recruitment data and that various populations are exposed to different numbers of dams, much in the spirit of the staircase experimental design method of Walters et al. (1989). An important set of our models rely on the hypothesis that Snake River and lower Columbia River spring and summer chinook salmon populations share a "common" mortality factor that can be used to partition total mortalities, as found in Schaller et al. (1999); Zabel and Williams (2000) contest that hypothesis and Schaller et al. (2000) respond to the contest. We refer the reader to those papers and to that of Marmorek et al. (1998) for background about why one might expect that similarities between Snake River and lower Columbia River chinook salmon populations could be exploited in order to characterize the remaining contrasting features of those populations.

We expand population modeling beyond the simple types of population models considered for Snake River and Columbia River chinook salmon in Schaller et al. (1999) and Botsford and Paulsen (2000). The primary model considered here is a generalization of the Ricker spawner and recruit model designed to accommodate a suite of factors thought to be important to the survival of the fish including year-specific factors for in-river passage mortality. Several alternative models can be structured by making alternative as-

sumptions about terms in the primary model. This paper differs from others on the same salmon population (Schaller et al. 1999; Botsford and Paulsen 2000) in that we compare and test several alternative assumptions about the structure of a single general model and the types of errors that need to be accommodated in the modeling. We believe that our use of a general population model offers advantages over correlation analysis of salmon survival trends, as for example in Peterman et al. (1998) or in Botsford and Paulsen (2000), in that we are able to change assumptions about error sources and multiple factors simultaneously. A disadvantage to our approach is that even a general model is limited to only a subset of possible hypotheses about error structure and factors. Another disadvantage is that it can be too time consuming to explore all possible permutations of assumptions.

Methods

Spring and summer chinook salmon populations

We analyzed data for 13 populations of chinook salmon (Table 1) for which time series of spawner and recruitment information were available at the time of this analysis (Beamesderfer et al. 1997). Down-river stocks included those of the Wind, Klickitat, and Warm Springs rivers and three populations in the John Day sub-basin system (John Day Mainstem, John Day Middle Fork, and John Day North Fork). The seven up-river stocks were from the Minam (a tributary of the Grande Ronde), the Imnaha (a tributary of the Snake River), and Bear Valley, Marsh Creek, Sulphur Creek, Poverty Flat, and Johnson Creek (tributaries of the Salmon River). The stocks of the up-river sub-basins migrate past more dams than do the down-river stocks (Table 1). Recruitment refers to year-class abundance of each stock when they return to the Bonneville Dam on the lower Columbia River.

Estimates of recruitment are back-calculations based on expansion of spawner estimates to account for losses that occur during the migration of salmon from Bonneville Dam to their spawning ground. Spawner estimates are estimates of annual abundance of sexually mature salmon at their respective spawning grounds. More specifically, Beamesderfer et al. (1997) estimated numbers of spawners and returning recruits to the mouth of the Columbia River for the upstream and downstream salmon populations using spawning-ground surveys, age frequencies, mainstem and tributary harvest rates, and mainstem conversion rates for upstream passage of adults. They gathered this information from historical data sets, reports, and ongoing monitoring. A major goal of their analysis was to develop a consistent methodology for reconstructing spawner and recruit data across index stocks. As with any reconstructed data set of this spatial and temporal breadth, assumptions were necessary. Although these assumptions and data sources are thoroughly documented, they do introduce additional uncertainty.

A thorough discussion of the reconstruction methodology and data quality issues is beyond the scope and intent of this paper. However, we note that these data have been used in several recently published analyses (e.g., Schaller et al. 1999; Botsford and Paulsen 2000; Petrosky et al. 2001). Their quality and influence on model parameter estimates and analytical inferences has been debated both during the PATH process (Marmorek and Peters 2001) and in the subsequent published literature (response of Schaller et al. (2000) to Zabel and Williams (2000); Deriso 2001; Hinrichsen 2001). We direct interested readers to these papers and to the PATH literature for further elaboration of the strengths and potential weaknesses of these data. In particular, Schaller et al. (1999) provides an excellent overview of the rationale and methods used by Beamesderfer et al. (1997). The full analysis of Beamesderfer et

Table 1. Summary information on the 13 chinook populations analyzed in this study.

Region	Sub-basin	Brood years of paired spawner–recruit data	Number of mainstem dams below sub-basin
Lower river	1. Wind	1973–1990	1
	2. Klickitat	1966–1990	1
	3. Warm Springs	1969–1990	2
	4. John Day Mainstem	1959–1990	3
	5. John Day Middle Fork	1959–1990	3
	6. John Day North Fork	1959–1990	3
Snake River	7. Imnaha	1952–1990	8
	8. Minam	1954–1990	8
	9. Bear Valley	1957–1990	8
	10. Marsh Creek	1957–1990	8
	11. Sulphur Creek	1957–1990	8
	12. Poverty Flat	1957–1990	8
	13. Johnson Creek	1957–1990	8

al. (1997) and the PATH literature are available at <http://www.efw.bpa.gov/Environment/PATH/>.

Population models

We focus on stock and recruitment models that assume that survival rates of chinook from rivers of the Snake and Columbia systems share many similar aspects. In particular, ocean mortality rates are assumed to share many common attributes across stocks from different streams. By making this assumption, differential mortality between up-river and down-river stocks can be attributed to differences in their in-river passage. To accommodate this assumption, our general model contains an optional year-effect component to reflect common factors affecting survival of all stocks.

The general model structure is based on a Ricker-type spawner–recruitment model that explicitly accounts for measurement error:

$$(1) \quad y_{t,i} = x_{t,i} + a_{t,i} - b_i e^{x_{t,i}} - m_{t,i} + \varepsilon_{t,i}$$

$$(1a) \quad \ln(S_{t,i}) = x_{t,i} + \varepsilon'_{t,i}$$

for which $y_{t,i}$ is the logarithm of recruitment; $R_{t,i}$ is the Columbia River “observed” recruitment originating from spawning in year t and river sub-basin i (number of fish); $S_{t,i}$ is the “observed” spawning in year t and river sub-basin i (number of fish); $x_{t,i}$ is the logarithm of “true” spawning; $a_{t,i}$ is the Ricker a parameter which depends on year and sub-basin (per year); b_i is the Ricker b parameter (1/number of fish); $m_{t,i}$ is the total passage mortality (direct dam mortality + differential mortality), which depends on year and sub-basin (per year); $\varepsilon_{t,i}$ is a normally distributed mixed process error and recruitment measurement error term $N(0, \sigma_\varepsilon^2)$ (per year); $\varepsilon'_{t,i}$ is a normally distributed spawner enumeration measurement error term $N(0, \sigma_\varepsilon^2)$ (per year); t is the year; and i is the sub-basin.

Chinook salmon may return to spawn at ages 3, 4, or 5, but our model does not contain separate mortality terms for each age-class of a given brood. Instead, we assumed a constant post-age-4 ocean survival. Interannual variation in marine survival is confined to the first 2 years of life in the estuarine and ocean environment. In their final years at sea, ocean mortality for chinook salmon is probably lower and not likely to induce large systematic variation in total ocean mortality (Schaller et al. 1999).

Density-independent mortality

Equation 1 combines all non-dam, density-independent mortality sources into a single parameter $a_{t,i}$, except for the additive process error $\varepsilon_{t,i}$. Thus, the a parameter contains a sum of egg-to-fry, fry-to-smolt, and smolt-to-adult density-independent mortality. The

density-dependent parameter b is chosen to be area specific to reflect the different carrying capacities of different areas. Typically, estimates of the a and b coefficients are confounded so we did not attempt to model temporal changes in carrying capacity explicitly.

We added structure for the a parameters in three alternative ways:

$$(2) \quad a_{t,i} = a + \delta_t$$

$$(3) \quad a_{t,i} = a_i + \delta_t$$

$$(4) \quad a_{t,i} = a_i + \delta_{t,\text{region}}$$

where for each alternative the parameter a is the Ricker a parameter, i is the sub-basin (e.g., Imnaha), and “region” refers to either the up-river or the down-river sub-basins. In eq. 2, the model assumes the same Ricker a value for all stocks except for Wind because it is an introduced stock (Schaller et al. 1999). In eq. 3, the model allows the Ricker a parameter to vary for each stock. We included the year-effect parameter δ_t to allow for year-effects common to all stocks; this would include major ocean mortality changes that affect the survival of chinook salmon during the first 2 years of ocean life, as well as regional changes in terrestrial climate that affect all stocks. Above-average climate conditions have $\delta_t > 0$, whereas below-average conditions have $\delta_t < 0$. Using either eq. 2 or eq. 3 as part of the overall model in eq. 1 requires the assumptions that (i) year-to-year variations in climate that effect the ocean survival of all stocks will be picked up by the year-effect δ_t ; (ii) random variations among stocks in ocean survival (owing to, for example, different ocean distributions or timing of ocean entry) will be assigned to the term $\varepsilon_{t,i}$ in eq. 1, which picks up any unexplained natural variation in survival during a fishes life until recruitment as well as recruitment measurement error; and (iii) variations among stocks in ocean survival are not systematic differences between up-river and lower-river stocks as regional stock groups.

To examine the sensitivity of the model to the third assumption, we added eq. 4, a generalization of eq. 3 that allows year-effects to differ between the up-river and lower-river stocks. When eq. 4 is implemented, an additional sum-of-squares (SSQ) term is needed in the estimation procedure to characterize the correlation between the year-effects in the two stock groups. If the within-region differences among stocks in year-effects are as large as the among-region differences, then these random effects will be assigned to the residual variation term $\varepsilon_{t,i}$. In such a case, there is no confounding of differential mortality estimates. However, in the special case where there are systematic differences between the year-effects of up-river stocks and those of lower-river stocks (i.e., differences between stock groups are significantly greater than those

within each stock group), then there is confounding of the parameter estimates for the up-river differential mortality and the region year-effects.

Eliminating spawner measurement error ($\epsilon'_{t,i}$ in eq. 1a), combining eqs. 1, 1a, and 3, and rearranging terms generates the following equation for our primary model:

$$(4a) \quad \ln(R_{t,i}/S_{t,i}) = (a_i + \delta_t - m_{t,i}) - b_i S_{t,i} + \epsilon_{t,i}$$

Equation 4a contains the following parameters that need to be estimated: δ_t , a_i , b_i , $m_{t,i}$, and the "true" spawning population abundances ($x_{t,i}$ in eq. 1a). Equation 4a is identical in structure to the multiple regression model commonly used to estimate the parameters of the Ricker model (Ricker 1975). The four major differences between our models and the standard Ricker model are as follows: (i) the inclusion of spawning enumeration measurement errors as estimated parameters; (ii) the specific independent variables used to explain variation in $\ln(R_{t,i}/S_{t,i})$ (i.e., right side of eq. 4a); (iii) the use of maximum likelihood estimation (MLE) procedures; and (iv) the grouping of stocks and years for the purposes of parameter estimation. Exponentiating both sides of eq. 4a generates the familiar Ricker equation plus two additional terms for the year and differential mortality effects:

$$(4b) \quad R = S e^{a_i - b_i S_{t,i} + \epsilon_{t,i} + \delta_t - m_{t,i}}$$

Exponentiating δ_t and $m_{t,i}$ expresses these parameters as fractional factors which in any given year can increase or decrease the recruitment from that expected by the Ricker parameters alone:

$$(4c) \quad R = S (e^{a_i - b_i S_{t,i} + \epsilon_{t,i}}) (e^{\delta_t}) (e^{-m_{t,i}})$$

Differential mortality (μ)

The emphasis of this study was the estimation of the differential mortality experienced by Snake River chinook populations from their sub-basins up to the John Day Dam for each brood year from 1970 to 1990. To do this, we used four alternative approaches to parameterizing m . The first approach uses a two-level parameterization scheme in which we separated dam mortality into two categories, as indicated by the Xs and Ys in Table 2 and referred to below as X-type and Y-type dam mortality. We assume that $m_{t,i}$ in eq. 1 is computed by

$$(5) \quad m_{t,i} = X \cdot n + \mu_t$$

where n is the number of X-type dams in Table 2 (John Day to Bonneville after 1970), X is the dam passage mortality associated with each X-type dam, and μ_t is the differential mortality from the Snake River sub-basins to John Day Dam (Y-type dams in Table 2), expressed as an instantaneous mortality rate for brood years $t \geq 1970$. Years shown in Table 2 are based on the year of initial service of each dam, lagged by 2 years to standardize to brood year (Snake River spring and summer chinook migrate down river as smolts 2 years after they are spawned). The first level of parameterization (number of Xs in each row of Table 2) treats mortality as a process proportional to the number of dams passed by juvenile salmon during their transit to the ocean, excluding those dams and (or) populations treated in the second level. At the second level of parameterization (Ys in Table 2), the differential mortality experienced by upstream stocks is estimated by μ_t , which we assume is ≥ 0 . The μ term is a "net" effect mortality estimate because it reflects the overall impacts of dam passage over the complete life cycle. This includes direct losses owing to trauma at the point of dam passage, increased "natural" mortality (e.g., predation) resulting from longer smolt residence time in dam reservoirs, latent mortality owing to the weakened condition of smolts, and the benefits or

detriments of transportation by barge for some Snake River smolts down river to below the Bonneville dam.

Mortality in any given year for any given population is obtained in Table 2 by adding the number of X dams encountered by that stock (n in eq. 5) and multiplying that by a mortality rate per dam, plus a second-level annual term for μ_t , provided that at least one Y dam is encountered by that stock. The Warm Springs stock, for example, which currently passes through only Bonneville and Dalles dams, would currently have $n = 2$ (Bonneville and Dalles dams) and $\mu_t = 0$. Johnson Creek, however, which passes through all eight dams, would have $n = 3$ (Bonneville, Dalles, and John Day) and an estimate of μ_t over five dams (McNary, Ice Harbor, Lower Monument, Little Goose, and Lower Granite).

The weakness of the first parameterization approach is that all per-dam mortality rates for the X dams are the same; there is no variation among dams or years. In the second parameterization approach, we address this weakness by using time-series estimates of total direct passage mortality ($M_{t,i}$) from the CRiSP (Columbia River Salmon Passage; Anderson et al. 1996) and FLUSH (Fish Leaving Under Several Hypotheses; Wilson 1994) passage models to create more flexible estimates of mortality for the dams and years with Xs in Table 2. The term $M_{t,i}$ is the total direct passage mortality from Lower Granite Dam (the first dam encountered by Snake River fish) to Bonneville Dam (the last dam encountered before fish reach the ocean); it is a weighted average of the dam and reservoir mortality experienced by nontransported fish and the barge mortality experienced by transported fish. The approach is to replace ($X \cdot n$) in eq. 5 by passage mortality proportional to that generated by the CRiSP or FLUSH models for the X dams only:

$$(6) \quad m_{t,i} = q M_{t,i} + \mu_t$$

where q is a proportionality constant (estimated in the MLE procedure) to be multiplied by the passage mortality from CRiSP and FLUSH for X-type dams. Including a proportionality constant allows the estimation algorithm to mimic the pattern of mortality changes in CRiSP-FLUSH, scaling up or down as required, without constraining the estimated mortality to be the actual value predicted by the passage models. The CRiSP-FLUSH model estimates include both dam-induced effects within the river system and a background level of "natural" mortality within the river passage. Some natural mortality between John Day Dam and Lower Granite Reservoir would be expected even without any dams along the Columbia River (0–20%; Toole et al. 1996). Therefore, a reduction of the CRiSP-FLUSH estimated mortalities by 0.0 to 0.2 would be needed to make them strictly comparable to the μ_t estimates, which only consider the differential mortality caused by downstream passage.

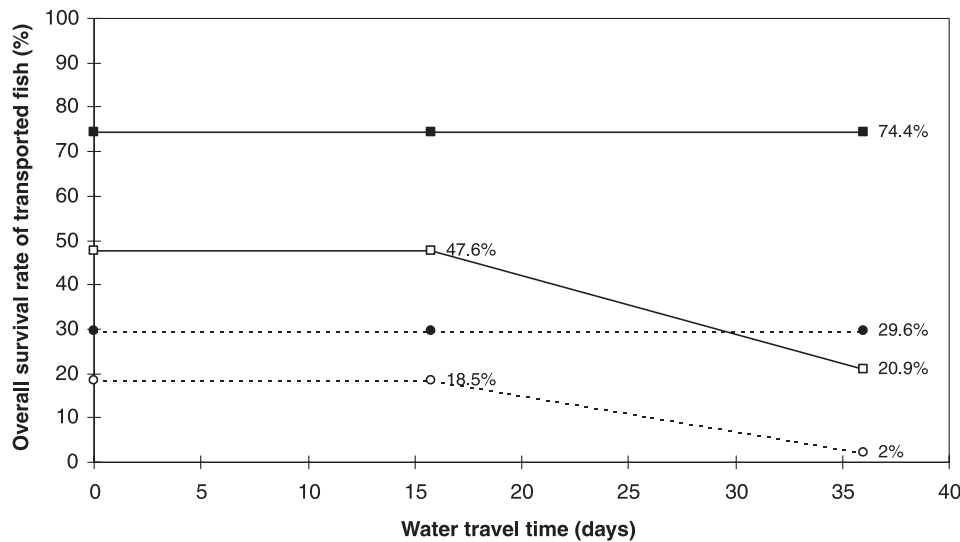
The third approach is to eliminate μ_t from eq. 6 and estimate $m_{t,i}$ for all of the dams passed by a given stock using estimates from passage and transportation models, either with or without the proportionately constant q . Two transport survival assumptions were applied to CRiSP and FLUSH, which led to four estimates of total direct passage mortality (Fig. 1). The transport survival assumptions are based on the ratio of survival of transported fish to non-transported (in-river) fish (transport-control ratio or T:C) in selected years of experiments, multiplied by the survival rate of in-river fish estimated by each passage model for those years. Transport survival therefore reflects smolt survival in the barge or truck, adjusted by the inferred relative survivals of transported and in-river fish after the last dam. Transport model 1 (T1) assumes that survival varies with water travel time (WTT), the average number of days that it takes a particle of water to get from the head of Lower Granite Reservoir to below Bonneville Dam during the spring migration period). The slope of the relationship is anchored at the high end by transport survival estimates using T:C values of 1.0:1 in 1986 (a high-flow, low-WTT year) and at the low end by trans-

Table 2. Types of passage mortality estimates.

Brood year(s)	Dams							
	BON	TDD	JDA	McN	IHR	LOMO	LGS	LGR
1952–1954	X			X				
1955–1958	X	X		X				
1959–1965	X	X		X	X			
1966	X	X	X	X	X			
1967	X	X	X	X	X	X		
1968–1969	X	X	X	X	X	X	X	
1970–1972	X	X	X	Y	Y	Y	Y	
1973–present	X	X	X	Y	Y	Y	Y	Y

Note: For the simplest models, X = fixed estimate of mortality/dam; Y = annually varying estimates of mortality resulting from passage through five dams; BON, Bonneville; TDD, Dalles; JDA, John Day; McN, McNary; IHR, Ice Harbor; LOMO, Lower Monumental; LGS, Little Goose; LGR, Lower Granite). More complex models replace the Xs with estimates either proportional or equal to CRiSP–FLUSH mortality estimates.

Fig. 1. Comparison of CRiSP (Columbia River Salmon Passage) and FLUSH (Fish Leaving Under Several Hypotheses) transport model survival assumptions. Model T1 assumes that transport survival decreases with water travel time, whereas model T2 assumes constant survival. FLUSH T2, ●; FLUSH T1, ○; CRiSP T2, ■; CRiSP T1, □.



port survivals using a T:C value of 3.0:1 in 1977 (a low-flow, high-WTT year). Transport model 2 (T2) assumes fixed survival, calculated based on a T:C of 1.6:1 for 1986 (this represents a point estimate for release to return at Little Goose Dam, the lower T:C in 1986 for T1 reflects survival to the spawning grounds). For both sets of assumptions, FLUSH clearly estimated much lower transport survival than CRiSP (Fig. 1). Revised versions of CRiSP, FLUSH, and the transportation models have been distributed since this analysis was completed (Peters and Marmorek 2001). However, the same general patterns still hold: CRiSP estimates of transport survival rate are generally much higher than FLUSH estimates.

The fourth approach again uses the two-level approach described in eq. 5 except that μ_t is assumed to be proportional to WTT. WTT is a candidate variable because longer travel times expose smolts to reservoir predators for longer periods and cause fish to experience more delays when passing dams. Transported fish may also reach the point of transport in poorer condition in low runoff years (high WTT), consistent with the general pattern in model T1 (Fig. 1).

Likelihood function and bias correction procedure

A set of 37 spawner–recruit models were developed, each representing a different combination of assumptions about spawner mea-

surement error, parameterization of Ricker a , parameterization of m , and the commonality of year-effects (Table 3). We calculated likelihoods for each model using a likelihood function made up of two parts: the normal errors for the usual error term in a Ricker model $\epsilon_{t,i}$ and the normal errors for the spawner measurement error $\epsilon'_{t,i}$. MLE estimates for all parameters are obtained by minimizing the negative log-likelihood function, which reduces to minimizing the following sum-of-squares:

$$(7) \quad SSQ = \sum \epsilon_{t,i}^2 + \lambda_{\epsilon'} \sum \epsilon'_{t,i}^2$$

where the variance ratio $\lambda_{\epsilon'} = \sigma_{\epsilon'}^2 / \sigma_{\epsilon}^2$ is specified a priori. Spawner-measurement error was estimated to have a coefficient of variation of 24%, based on a comparison of redd counts to weir counts in the Lemhi River (C. Petrosky, Idaho Department of Fish and Game, 600 S. Walnut, Boise, ID 83707, personal communication). Preliminary analyses showed that process error had a variance slightly larger than the measurement error variance and $\lambda_{\epsilon'}$ was set equal to 1.5 in models for which both error terms were estimated. The likelihood function for the model that includes regional year-effects (i.e., eq. 1 with eq. 4 for $a_{t,i}$) contains an additional SSQ term:

Table 3. Results of applying 37 different models to stock and recruitment data.

Model number	Spawning measure error?	Different <i>a</i> ?	Distinguishing features	Total sums of squares
1*	N	Y	Eq. 5 total passage mortality (<i>m</i>)	111.88
2	Y	Y	Eq. 5 total passage mortality (<i>m</i>)	92.14
3*	N	N	Eq. 5 total passage mortality (<i>m</i>)	120.07
4	Y	N	Eq. 5 total passage mortality (<i>m</i>)	96.3
5*	N	Y	X-type dam mortality proportional to CRiSP T1	111.49
6*	N	Y	X-type dam mortality proportional to CRiSP T2	111.47
7	N	Y	X-type dam mortality proportional to FLUSH T1	113.09
8	N	Y	X-type dam mortality proportional to FLUSH T2	113.09
9	N	Y	<i>m</i> passage mortality rate proportional to CRiSP T1	149.27
10	N	Y	<i>m</i> passage mortality rate proportional to CRiSP T2	157.06
11*	N	Y	<i>m</i> passage mortality rate proportional to FLUSH T1	141.49
12	N	Y	<i>m</i> passage mortality rate proportional to FLUSH T2	152.67
13	N	Y	<i>m</i> passage mortality rates = CRiSP T1 values	153.19
14	N	Y	<i>m</i> passage mortality rates = CRiSP T2 values	179.72
15	N	Y	<i>m</i> passage mortality rates = FLUSH T1 values	155.02
16	N	Y	<i>m</i> passage mortality rates = FLUSH T2 values	164.07
17	N	Y	<i>m</i> = X·(total number of dams passed)	149.99
18*	N	Y	(Same as No. 13 CRiSP T1), except exclude BY 1971	147.62
19	N	Y	(Same as No. 14 CRiSP T2), except exclude BY 1971	174.02
20*	N	Y	(Same as No. 15 FLUSH T1), except exclude BY 1971	141.95
21*	N	Y	(Same as No. 16 FLUSH T2), except exclude BY 1971	146.86
22	N	Y	Sub-basin year-effects; <i>m</i> as in No. 1; λ(basin) = 0.01	107.12
23	N	Y	Sub-basin year-effects; <i>m</i> as in No. 1; λ(basin) = 1.0	108.64
24	N	Y	Sub-basin year-effects; <i>m</i> as in No. 13; λ(basin) = 0.01	106.51
25	N	Y	Sub-basin year-effects; <i>m</i> as in No. 13; λ(basin) = 1.0	118.62
26	N	Y	Sub-basin year-effects; <i>m</i> as in No. 14; λ(basin) = 1.0	126.42
27	N	Y	Sub-basin year-effects; <i>m</i> as in No. 15; λ(basin) = 1.0	119.32
28	N	Y	Sub-basin year-effects; <i>m</i> as in No. 16; λ(basin) = 1.0	121.62
29	N	Y	<i>m</i> = X·(total number of dams passed); no year-effect	299.48
30	N	Y	No year-effect; <i>m</i> as in No. 11, FLUSH T1	289.89
31*	N	N	<i>m</i> passage mortality rate proportional to CRiSP T1	154.17
32	N	N	<i>m</i> passage mortality rate proportional to CRiSP T2	167.17
33*	N	N	<i>m</i> passage mortality rate proportional to FLUSH T1	149.53
34	N	N	<i>m</i> passage mortality rate proportional to FLUSH T2	158.23
35	N	N	<i>m</i> = X·(total number of dams passed)	158.56
36*	N	N	μ passage mortality rate proportional to WTT	145.82
37*	N	Y	μ passage mortality rate proportional to WTT	136.28
			Average across all models	144.59
			Median value	145.82

Note: Top models (* after model number) have AIC and BIC values below the median for all models. WTT is water travel time. Equation 1 applies to defined by eqs. 7 and 7a. Number of parameters are obtained by counting parameters in eq. 1, configured with the appropriate optional equations listed in eqs. 7 and 8. Average μ is the average of the estimates in eq. 5 for brood years 1970–1990. The average Ricker *a* parameter is obtained by averaging Under Several hypotheses; Y, yes; N, no.

$$(7a) \quad SSQ = \sum \varepsilon_{t,i}^2 + \lambda_{\varepsilon'} \sum \varepsilon'_{t,i}^2 + \lambda_{\text{region}} \sum (\delta_{t,\text{region1}} - \delta_{t,\text{region2}})^2$$

in which λ_{region} is the variance ratio (similar to λ_{ε'}), δ_{t,region1} is the year-effect for lower-river stocks and δ_{t,region2} is the year-effect for up-river stocks. The variance ratio term λ_{region} was set to 1.0 because we had no better estimate.

The MLE estimates were obtained by application of a Marquardt nonlinear minimization routine (Draper and Smith 1966). We applied a Monte Carlo bootstrap procedure (Efron 1979, 1981) to the MLEs to produce median unbiased estimates. The bootstrap method is identical to the one described in Deriso et al. (1985) in

which we sample, with replacement, the residuals from the original model fitting, generate pseudo-observed data, and then fit the model to pseudo-observed data, repeating this process 100 times. Median estimates from the bootstrap trials provide an estimate of bias for the original MLEs. The bias appears to be rather minor in the results (usually less than 10% of the estimated quantity). Therefore, a first-order procedure such as the bootstrap procedure appears to be a reasonable approach in this case, although the method may not work well with other data sets that exhibit larger bias (C. Walters, 2204 Main Mall, University of British Columbia, Vancouver, BC V6T 1Z4, personal communication; J. Collie, University of Rhode Island, Narragansett, RI 0882-1197, personal communication). All model results reported here were corrected for bias by subtracting the estimated bias from the MLE estimates.

Number of parameters estimated	Number of likelihood components	Akaike information criterion (AIC)	Bayesian information criterion (BIC)	Average μ	Average Ricker a parameter
86	406	800.7	1145.2	1.44	2.65
492	812	1520.9	3833.0	1.26	2.45
75	406	807.4	1107.8	0.82	1.84
492	823	1553.4	3872.2	0.81	1.84
86	406	799.3	1143.8	1.07	2.12
86	406	799.2	1143.7	1.07	2.13
86	406	805.0	1149.6	1.02	1.97
86	406	805.0	1149.6	1.02	1.97
65	406	875.7	1136.1	0.59	1.95
65	406	896.4	1156.8	0.02	1.53
65	406	854.0	1114.4	0.99	2.03
65	406	884.9	1145.3	0.54	1.81
64	406	884.3	1140.7	1.00	2.26
64	406	949.1	1205.5	0.48	2.04
64	406	889.1	1145.5	1.90	2.51
64	406	912.1	1168.5	1.40	2.29
65	406	877.7	1138.1	1.44	2.68
63	393	856.3	1106.6	1.00	2.24
63	393	920.9	1171.3	0.48	2.02
63	393	840.9	1091.2	1.90	2.50
63	393	854.2	1104.6	1.40	2.27
118	438	861.9	1343.6	1.43	2.65
118	438	868.1	1349.8	1.44	2.65
96	438	815.4	1207.3	1.00	2.35
96	438	862.6	1254.5	1.00	2.32
96	438	890.5	1282.4	0.48	2.16
96	438	865.2	1257.1	1.90	2.48
96	438	873.6	1265.4	1.40	2.33
27	406	1082.4	1190.6	1.88	3.04
27	406	1069.2	1177.4	1.32	2.02
54	406	866.8	1083.2	0.55	1.89
54	406	899.7	1116.1	0.14	1.63
54	406	854.4	1070.8	0.71	1.85
54	406	877.4	1093.7	0.53	1.77
54	406	878.2	1094.6	0.57	1.94
55	406	846.2	1066.6	0.79	1.78
66	406	840.8	1105.2	1.34	2.52
94.14	432.89	909.16	1306.16	1.03	2.17
65	406	868.1	1145.3	1.00	2.13

all models. Entries in columns 2, 3, and 4 are variations on eq. 1 created using eqs. 1a, 2, 3, 4, 5, and 6. The total sums of squares is the sum of squares above, and counting numbers of stocks and years of data in Table 1 for the particular model. Number of likelihood components are the number of terms estimates across the seven sub-basin stocks in the Snake River region. BY, brood year; CRiSP, Columbia River Salmon Passage; FLUSH, Fish Leaving

Detailed testing over a range of dam mortalities and model structures indicated that the lowest bias models included estimates of X-dam mortality and stock-specific Ricker a values and assumed no spawner measurement error.

Ranking alternative models

We used two criteria for assessing the relative fits of each model to data: the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) (Akaike 1973; Kass and Raftery 1994). Better model fits correspond to lower AIC and BIC scores. The AIC, given by the equation

$$(8) \quad AIC = -2\ln(\text{likelihood}) + 2p$$

and the BIC, given by the equation

$$(9) \quad BIC = -2\ln(\text{likelihood}) + p\ln(k)$$

are both based on asymptotic properties of the likelihood function (p is the number of parameters estimated and k is the number of “observations”, where we count observation number as the number of SSQ components). Both the AIC and BIC use twice the log-likelihood, which is asymptotically a χ^2 statistic. Therefore, both statistics are also related to asymptotic likelihood ratio tests that use classical hypothesis testing to test nested models (Mood et al. 1974). Both the AIC and, to a much greater extent, the BIC correspond to a very small rejection criterion (probabilities below 0.005) for alternative nested models with 21 or more additional parameters in the larger model (as we have in this study). That is, neither the AIC nor BIC criteria will reject a simple model in favor

of a more complex model unless there is a significant improvement in SSQ ($p < 0.005$).

There are differing perspectives on which criterion should be used to select models (Kass and Raftery 1994). From a Bayesian perspective, Gelman et al. (1996) argue against model selection altogether, as the alternative models represent alternative hypotheses that should not be discarded. Instead, the model should be general enough to contain alternatives as special case solutions to allow calculation of posterior probabilities that reflect the relative credibility of alternative hypotheses. A reasonable compromise would be only to reject models that are grossly less supported by AIC and BIC but reserve judgement on the remaining ones.

Results

Relative fits of models to data

Relative fits of the 37 spawner–recruitment (S – R) models to the spring and summer chinook spawner–recruitment data series are shown in Table 3. The best (lowest) AIC scores occurred for models where μ was estimated each year (models 1, 3, and 5–8). Among those models, comparable AIC values were produced by models that parameterized X-dam mortality as a constant per-dam mortality and by models in which X-dam mortality was proportional to passage model estimates. The best (lowest) BIC scores occurred for models with fewer parameters (particularly models 33 and 36), although these models still included year-effect parameters. Simple parameterizations for μ were favored by the BIC criterion, either as μ proportional to WTT, as in model 36, or with total differential mortality m proportional to passage model values from CRiSP or FLUSH (models 31–34).

Based on the results in Table 3, we identified a set of 12 “top” models for which both the AIC and BIC were below the median for all 37 models. Top models were 1, 3, 5, 6, 11, 18, 20, 21, 31, 33, 36, and 37 from Table 3. All top models included a common year-effect and excluded spawner measurement error. Both assumptions about commonality of the Ricker a parameter were represented in the set of top models, as were all four approaches to estimating m . Parameter estimates for the top models support a wide range of alternative hypotheses about the magnitude of the up-river net differential mortality μ and Ricker a parameters. Average μ for the top models ranged from 0.55 to 1.90 (mean of 1.09), which corresponds to a range of 42–85% ($100(1 - e^{-\mu})$) mortality owing to downstream passage from Lower Granite to John Day dams, over the entire life cycle (mean of 66%). Average Ricker a values of these models ranged from 1.78 to 2.65 (mean of 1.92). The range in average production index ($a - \mu$) for these models was smaller, from 0.60 to 1.34 (mean of 1.06). The smaller range in average production reflected the correlation between estimates of μ and a , which was also present in the bootstrap simulations done for models 1 and 3. Higher differential mortality estimates required higher production values to match observed patterns in spawner–recruit data.

Temporal patterns in differential mortality, total passage mortality, and common year-effects

Time trends in μ and year-effects for a subset of three of the models are shown in Fig. 2. These models were typical of ones for which both a year-effect and yearly μ parameter were

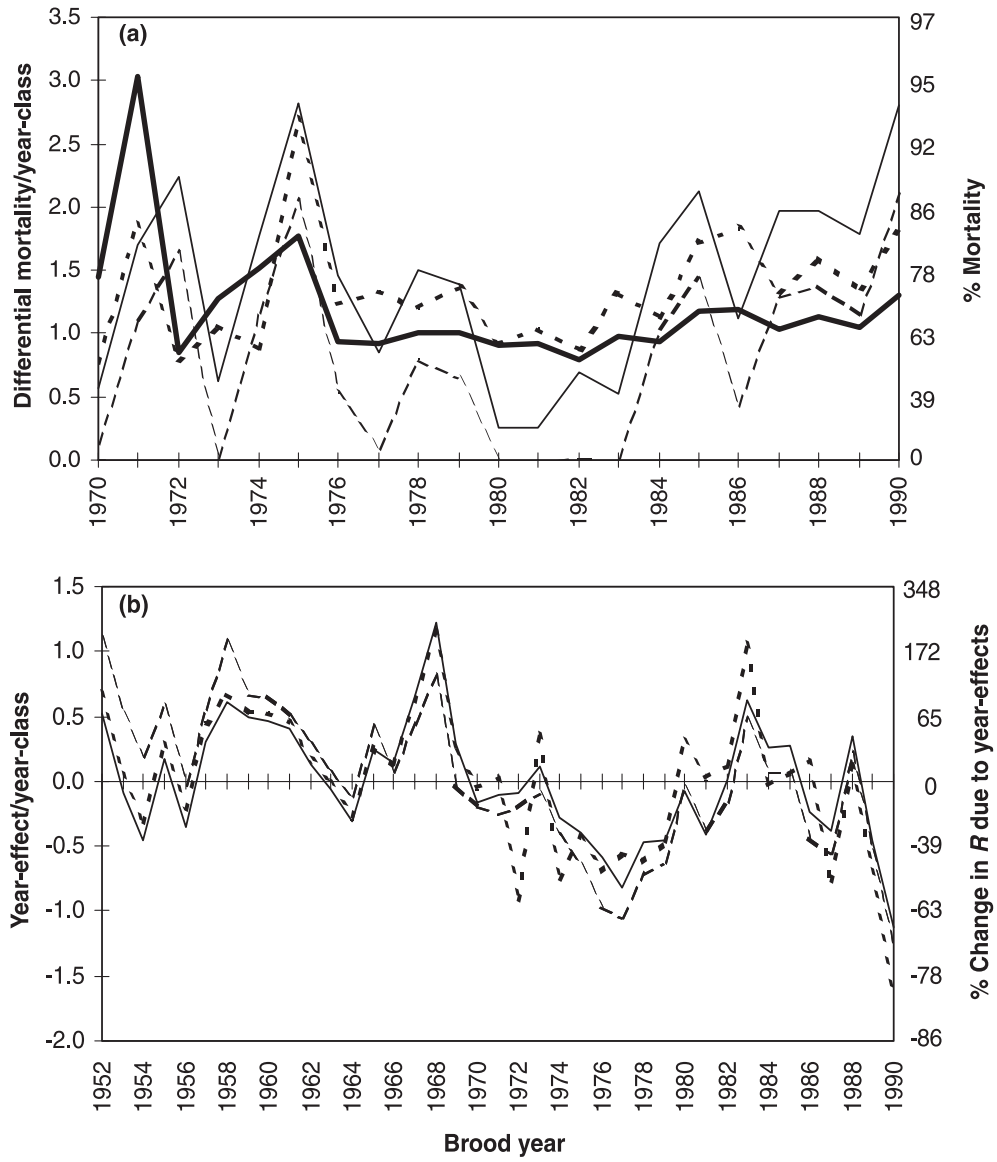
estimated. Models 1 and 4 used the first parameterization of differential mortality given above (i.e., eq. 5; constant mortality per project) but used different assumptions about inclusion of spawner measurement error and differences in Ricker a parameters among stocks. Model 1 did not include spawner measurement error and estimated a different Ricker a parameter for each stock. Model 4 included measurement error and estimated a single a parameter for all stocks. Overall, models 1 and 4 provided upper and lower bounds, respectively, on the μ values estimated by models 1 to 8 in Table 3, where models 5–8 used X-dam mortality proportional to the passage model estimates. The final model, number 37 of Table 3, was included in Fig. 2 because of its low BIC score and because it contained a simplified passage model: μ proportional to WTT. This model had a slightly higher BIC score than that of model 36 but was chosen because it included different Ricker a parameter values (shown in simulation tests to perform more accurately).

All three S – R models gave similar estimates of time trends both in μ (differential mortality from Snake River sub-basins to John Day Dam) and in δ_t (year-effect parameter) (Fig. 2). The time trend in μ was one of a cyclical high to moderate mortality throughout the 1970s followed by a 4-year period of low mortality (1980–1983), then a return to a stable but slightly cyclical mortality through the latter half of the 1980s, and an upward spike in 1990 (Fig. 2a). Figure 2a shows the average of the four CRiSP–FLUSH and T1–T2 differential mortality estimates (μ), whereas Fig. 3 shows each of these four models’ estimates of μ separately. Average passage model estimates of μ generally passed through the μ estimates of the four S – R models with three notable exceptions: (i) the spiked mortality indicated by the passage models for brood year 1971 was not present in any of the S – R models (survival trends show that brood year 1972 was the poor year, not 1971, especially for the Bear Valley, Sulphur Creek, Poverty Flats, and Johnson Flats populations); (ii) the mortality indicated by the passage models for brood years 1980–1983 did not show the precipitous reduction in mortality (increase in survival) indicated in all S – R models; and (iii) the increased mortality in all eight models in 1990 was above the average passage model. A previous examination of the 4-year high survival result in 1980–1983 showed that the reduction in mortality for the up-river populations was due to both real increases in recruitment and decreases in spawning population. The decrease in spawning populations was also observed on the lower-river populations, but they did not experience the increase in recruitment that was seen in up-river populations. The four passage models showed substantial differences in estimated μ . Though the CRiSP T2 passage–transportation model also showed low μ (high survival) during 1980–1983, it did not show the subsequent increasing mortality indicated by the S – R models (Fig. 3). A moderate long-term cycle was present for estimated year-effects (Fig. 2b), indicating a shift in climate mortality regimes from a generally high positive anomaly sequence for the 1952–1968 brood years followed by generally negative anomalies for the 1970–1989 brood years.

Year-effects

There was strong support for inclusion of year-effects in

Fig. 2. (a) Estimates of differential mortality (μ) above John Day Dam by brood year for three stock–recruitment models (numbers 1, 4, and 37 in Table 3) and the average of estimates produced by four passage and transport models. The second y axis converts μ to an estimated percent mortality over the complete life cycle ($100(1 - e^{-\mu})$). (b) Year-effect (δ) estimates for the same three stock–recruit models (year-effects were not estimated by passage and transport models). The second y axis converts δ to an estimated percent change in recruitment ($100(e^{-\delta} - 1)$). Model 1, thin solid line; model 2, thin broken line; model 37, thick broken line; average passage model (Fig. 2a only), thick solid line.



the models, as seen by the high AIC and BIC scores (poorer fits) for models 29 and 30 in which no year-effect was included. Regional year-effects were investigated in models 22 to 28. BIC scores for those regional models were substantially poorer than models without region-specific year-effects (models 1 and 13–16 in Table 3). AIC scores were poorer for models 22 and 23 than for model 1, one of the better empirical models. However, the CRiSP- and FLUSH-based models showed lower AIC values when region-specific year-effects were included (models 24–28 vs. 13–16), perhaps because this gave more flexibility to accommodate upstream–downstream differences in survival. Differential mortality rates were very similar between those two types of

models, whereas the regional models estimated a slightly larger average Ricker a parameter.

Correlation between variables

Using model 1, we examined estimates of μ (differential mortality) and δ (common year-effects) for correlations with other variables. There was a significant positive correlation ($r = 0.58, p < 0.01$) between μ and WTT (Fig. 4). The correlation was weaker but still significant even without the influential 1975 brood year ($r = 0.45, p < 0.05$). Some pairs of years with very similar WTT had very different values for μ (e.g., 1970 vs. 1972, 1974 vs. 1980, 1983 vs. 1989, and 1986 vs. 1990), suggesting that other factors besides WTT

Fig. 3. Comparison of median estimates of differential mortality (μ) using model 1 from Table 3 (thick, solid line), with estimates of μ from four mechanistic passage models (FLUSH T1, ●; FLUSH T2, ○; CRiSP T1, ■; CRiSP T2, □). The second y axis converts μ to an estimated percent mortality over the complete life cycle ($100(1 - e^{-\mu})$).

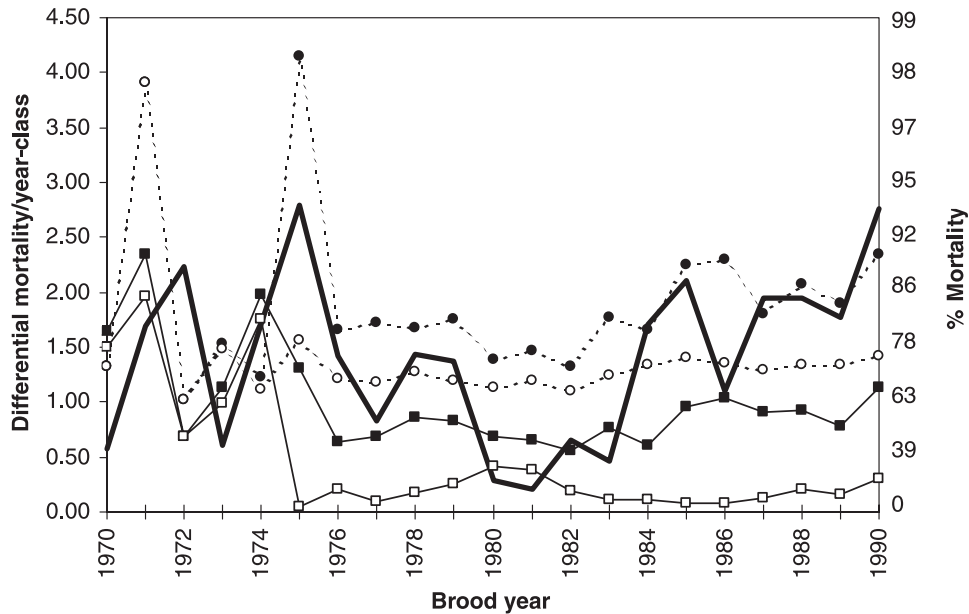
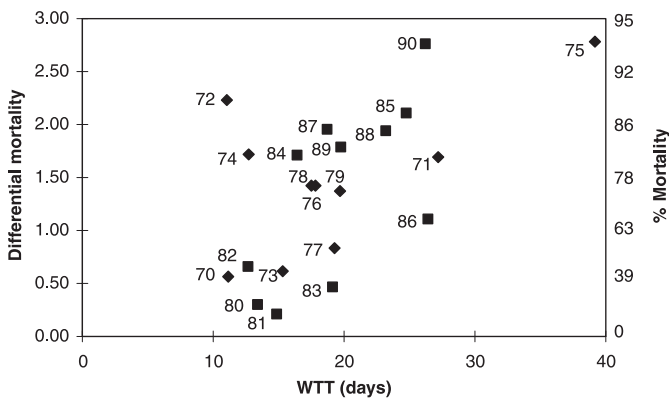


Fig. 4. Estimated differential mortality (μ) vs. water travel time (WTT). The regression line was fit through all of the data. The second y axis converts μ to an estimated percent mortality over the complete life cycle ($100(1 - e^{-\mu})$). Solid diamonds represent the 1970s brood years; solid squares represent the 1980+ brood years.



influenced the value of μ in these years (Fig. 4). We separated the 1970–1979 and 1980–1990 periods to see if differences in power system management or other factors may have affected the correlation between WTT and μ . The 1970–1979 period showed a weaker correlation ($r = 0.58, p = 0.08$; without the 1975 datum $r = 0.06, p = 0.87$) than the 1980–1990 period ($r = 0.68, p = 0.02$). However, an analysis of covariance with WTT as the covariate showed no significant difference between the 1970s and 1980s ($p = 0.623$).

The year-effect (δ) reflects common factors affecting survival of all stocks. We therefore selected two general climate indicators (the North Pacific Index (NPI; Trenberth and Hurrell 1994) and an Upwelling Index) and WTT to see if they were correlated with δ . Correlation between δ and WTT was not significant ($r = -0.15$). NPI showed low correlations in all cases when matched to the first, second, and third ocean

winter (i.e., $r = 0.08, 0.26, \text{ and } 0.33$, respectively). The Upwelling Index was also not correlated with δ ($r = -0.09$). Interestingly, the standardized residuals of Bristol Bay sockeye survivals (Peterman et al. 1998) were negatively correlated with δ ($r = -0.51$). This is consistent with the hypothesis that ocean conditions experienced by salmon in the Northeast Pacific vary inversely with those experienced by salmon originating from Oregon and Washington (Mantua et al. 1997).

The correlation between MLE estimates of μ and δ ($r = -0.24$) in different years was not significant. Within-year estimates of the correlation of μ and δ were obtained by linear approximation around the MLE solution and are all moderately large numbers (around $r = 0.75$). The correlation structure presents a mixed picture: there is uncertainty about the relative influence of common year-effects and differential mortality within individual years, but the uncertainty is not so large as to support removal of year-effects from the model (compare models 29 and 30 with all others in Table 3). Between-year correlations are small so MLE estimates reasonably portray the larger pattern. The only obvious between-year pattern was that the brood year with the best year-effect (1983) also had a low differential mortality and the brood year with the worst year-effect (1990) also experienced high differential mortality.

Discussion

Stock–recruit models that best fit the spawner–recruit data included a common year-effect, excluded spawner measurement error, and included varying parameterizations of Ricker a and m . Our empirical estimates of differential mortality between upstream and downstream stocks with those models ranged from 42 to 85%. In general, MLE estimates of passage mortality from the empirical model 1 are intermediate between the CRiSP and FLUSH passage model estimates.

Mechanistic and empirical passage mortality estimates agreed better when mortality estimates from CRiSP and FLUSH were scaled. On the other hand, even the simple explanatory variable WTT could be used to model differential mortality with high performance (as in models 36 and 37).

The influence of in-river studies on the 1971 brood year (conducted on migrants in 1973, a low-flow year) has been profound in the debate over the effects of dams on mortality of smolts (e.g., Williams and Matthews 1995). Our results show that the 1973 study results are not consistent with observed returning recruits from the 1971 brood year. If the high mortality rate estimated by FLUSH for the 1971 brood year is correct (i.e., a differential mortality μ which is 3.4 above the μ given by model 1), then we must have had an exceptionally strong year-class for the 1971 brood year in terms of their natural survival to account for the observed spawner-to-recruit survival. In particular, the observed natural recruitment survival rate, $\ln(R/S)$ (i.e., excluding differential mortality) would have to be roughly 3.4 above the observed average R/S rate, which includes differential mortality. Adding 3.4 to the observed standardized $\ln(R/S)$ for brood year 1971 would place it about 1.0 above the maximum standardized survival for any other brood year for the up-river stocks. On the other hand, the high passage mortality for the 1975 brood year (1977 out-migration, another low-flow year) estimated by the passage models and by the empirical model 1 is generally consistent both with the observed $\ln(R/S)$ survival rate and with in-river studies conducted that year.

An alternative explanation for our results is that the decline in survival of up-river vs. down-river natural stocks was due to a marine mortality factor that differentially affected up-river and (or) down-river stocks in a large enough way to coincide with and account for the estimated differential mortality. However, models that included regional year-effects (models 22–28) generally performed worse than the empirical models that exclude this alternative hypothesis (e.g., model 1). In addition, despite intense scrutiny, within and outside of PATH, of this assumption using coded wire tag recovery data, no analyses to date clearly indicate systematic, regional differences between up-river and low-river stocks in ocean distribution or mortality (e.g., Marmorek et al. 1998; Schaller et al. 2000). Though it would be valuable to obtain better estimates of among-region differences in ocean distribution and survival of wild spring chinook, there are clearly not enough wild fish remaining to generate sufficient tag recoveries.

The models developed in this paper omit statistical covariance in the measurement errors. We did not attempt to model directly the process by which recruitment estimates were obtained by Beamesderfer et al. (1997), although such modeling is theoretically possible. The advantage of a more complete model for recruitment measurements is that we would then have the appropriate error structure for including the statistical covariance structure between recruitment measurement error and the several years of spawner-measurement error to which they contribute. Our opinion is that this covariance is likely low for two reasons. First, recruitment measurement errors originate from many important sources other than those induced by errors in escapement counts, including conversion rates applied at

each dam to convert dam counts to total passage estimates, age distribution data, and correction for hatchery fish, and harvest removal. Second, chinook salmon return to the Columbia River to spawn (and hence become part of recruitment) over 4 or more years and thus the spawner-measurement error calculated in any given year would be applicable only to a portion of the recruitment from a given brood year. Other concerns are the presence of covariance in recruitment measurement errors among populations that share nearby sub-basins (such as the Snake River populations). We examined autocorrelation between recruitments in adjacent years and found that it had a negligible effect. Finally, another concern is that John Day Middle Fork stock, if excluded from the analysis, greatly reduces MLE estimates of up-river differential mortality and some sources of measurement error have been identified for this stock (Hinrichsen 2001); that concern has been debated within PATH without any resolution.

There is clearly uncertainty about the magnitude of differential mortality, year-effects, and Ricker a parameters. One way to address that uncertainty is to construct a single model that encompasses a range of alternative hypotheses about those parameter values and then conduct analyses that formally incorporate the uncertainty. Such a model is our model 1, which contains year-specific differential mortalities, common year-effects, and individual stock Ricker a parameters. It is in a virtual tie for best model according to the AIC criterion. Deriso (2001) describes the mechanics of generating prospective analyses for spring and summer chinook by application of Bayesian methods to model 1. The prospective modeling is part of a formal decision analysis of management actions designed to recover listed Snake River spring and summer chinook populations (Peters and Marmorek 2001).

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