An analysis of smolt survival with implications to flow management

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Abstract

Smolt survival through the Columbia/Snake river hydrosystem and tributaries of the Snake River are evaluated with the XT-model, which describes predator-prey interactions in terms of migration distance and time, temperature, turbidity, and a random encounter velocity between predators and prey. In this formulation, smolt survival depends on both distance traveled and exposure time, and the importance of each depends on the amount and character of predator and prey motions. The model is used to analyze factors that determine survival characterized in a PIT tag database of over five thousand individual survival estimates derived from PIT tagged fish between 1995 and 2002. The analysis indicates chinook and steelhead survival through the hydrosystem depends on migration distance, temperature, and the amount of spill at dams. In the tributaries above Lower Granite Dam, spring chinook survival depends on distance traveled from the release sites above the dam. Steelhead survival depends on migration distance and migration time but is independent of temperature, flow and turbidity. Fall chinook survival above Lower Granite Dam depends on travel distance and time, temperature, and turbidity.

Evaluating the impact of flow augmentation and water withdrawals on smolt survival requires considering, first, how these flow management actions affect water velocity, turbidity and temperature, and second, how these properties affect smolt survival. The analysis suggests that flow management actions affect only fall chinook in the tributaries and that the impacts may be positive or negative. Furthermore, the analysis indicates that empirical regression techniques, without ecological foundations, are inadequate to understand and characterize the effects of water management actions of smolt survival.

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Introduction

In this manuscript, factors affecting the survival of juvenile salmon and steelhead migrating through Columbia/Snake river tributaries and hydrosystem are investigated. The analysis considers a large PIT tag database of fish released within and above the hydrosystem and recaptured at Snake and Columbia River dams. The intent of the study is to explore how environmental variables and hydrosystem operations affect smolt survival. The analysis addresses the effects of flow and other environmental variables on survival between years and within years.

Data on juvenile salmon migration through the Snake and Columbia Rivers is studied using an extension of a survival model recently developed (Anderson 2003, to be submitted to American Naturalists by Anderson and Zabel). In this model, smolt survival is described in terms of a dependence on distance traveled as well as travel time. The model, referred to as the XT model, was derived from molecular collision theory and was motivated by observations showing smolt survival through tributaries and the hydrosystem is not significantly related to smolt travel time (Bickford and Skalski 2000, Muir et al. 2001, Smith et al 2002). This finding at face value is perplexing since we expect that mortality of the migrating prey should increase with increased exposure to predators along the migration route. However, tagging studies of hatchery fish released in the Snake tributaries in particular show a significant relationship between migration distance and survival (Muir et al. 2001). In this manuscript, we extend the XT model, including temperature and turbidity to explore how these environmental factors are correlated with smolt survival.

A significant number of studies on the factors affecting smolt survival have been produced in both the referred literature and in special reports. These studies have explored the factors affecting survival through statistical regression models: in particular, multiple linear models in which survival, or log survival, is regressed against a number of independent variables such as travel time, temperature, turbidity or flow. The analysis reported here is unique in that the model is developed first from principles based on a theoretical model of how smolts interact with their predators.

Whereas the coefficients in empirical regression models have no precise ecological meanings, the coefficients of the XT model have specific ecological meanings. As such, the ranges of the coefficients in the XT models must fall within ranges permissible and realistic in terms of the ecological variables from which they are derived.

Survival Model

Ecological theory traditionally describes predator prey interactions in terms of a law of mass action in which the prey mortality rate depends on the density of predators and prey. In such models, the mortality rate is characteristically a function of the exposure time of the prey to predators. However, observations on migrating prey (juvenile salmon) through a field of predators (piscivors) reveals that mortality depends mostly on distance traveled and only weakly on travel time. The XT model based on gas collision theory reconciles these observations. In this formulation, survival depends on both distance traveled and exposure time, and the importance of each depends on the intensity and character of predator and prey motion. If prey migrate directly through a gauntlet of stationary predators the prey mortality depends on migration distance not migration time. This gauntlet effect provides an explanation for distance dependence of mortality in juvenile salmon migration. At the other extreme, if prey and predators move randomly within an enclosed habitat, mortality is time dependent. Spatiotemporal dimensions of the ecological neighborhood in which predation events occur are defined in terms of a predator-prey encounter area and the relative random velocity between the predator and prey. For the development of the XT model see Anderson (2003).

Theory

Because smolts migrating through the Snake and Columbia River hydrosystem pass through river reaches as well as dams, to evaluate the survival studies the survival of fish passing through dams, S_{dam}, must be added to the river survival S_{river}, which is expressed with the XT model. The total reach survival, S, is then

1) $$S = S_{river} S_{dam}$$

Dam survival is estimated separately using the standard equation in which survival depends on the operation and characteristics of each dam according to the equation

2) $$S_{dam,i} = \left(S_{bypass,i} * FGE_i + S_{turbine,i}(1 - FGE_i \right) * (1 - SF_i) + S_{spill,i} SF_i$$

where the subscript i refers to a particular dam, FGE is the fish guidance efficiency, characterizing the fraction of fish guided into the bypass system at a dam, SF is the fraction of fish passing in spill water at the dam, and S_{bypass}, S_{turbine}, and S_{spill} are smolt survivals through the dam bypass route, turbines and spillways. These passage route survivals, as well as *FGE,* have been estimated independently; here we use previously derived estimates, which are constants specific to each dam. Then dam survival is variable with the daily spill fraction SF. The total dam survival is the product of the individual dams so

3) $$S_{dam} = \prod_i S_{dam,i}$$

In the XT model survival is defined as (Anderson 2003)

4) $$S_{river} = \exp\left(-\frac{t}{\lambda} \sqrt{V^2 + \omega^2} \right)$$

where t is the travel time, V is the average smolt migration velocity, ω^2 is the mean squared *random* encounter velocity between predators and prey, and λ scales the size of the ecological neighborhood in which predator-prey events occur. Because the migration distance is the product of the average smolt migration velocity and the migration time, survival becomes a function of migration distance and travel time as

5) $$S_{river} = \exp\left(-\frac{1}{\lambda}\sqrt{x^2 + \omega^2 t^2}\right)$$

where x is the smolt migration distance.

In Eq.(5), ω partitions the effect of migration distance and travel time on survival. If ω is small, such that the random part of the predator-prey encounter velocity is small, then smolts essentially migrate through a gauntlet of stationary predators and their survival depends on the distance of migration, not how long it takes them to travel the gauntlet. Correspondingly, if ω is large the random velocities of the predators and/or prey are significant, and a prey may have frequent encounters with a predator; so prey survival depends on the total exposure time and less on the migration distance.

The scaling term for the ecological neighborhood, λ, represents the relative length or distance between predator and prey. The length scale is defined in terms of the cross-sectional area of a predator prey encounter, α, in which predation events occur, and the effective predator density, ρ in the ecological neighborhood. These terms are related $\lambda = 1/\alpha\rho$. Thus, lower densities and small encounter areas result in large path lengths and lower mortality rates. While in the original formulation (Anderson 2003) the encounter area and predator density were constant, here we extend the model to incorporate environmental properties into the ecological neighborhood scale. In a generic form, we expresses this scale

6) $$\lambda = \delta / f(\Theta)$$

where $f(\Theta)$ is a generic function expressing how the ecological neighborhood scale changes with environmental covariates Θ, and δ is a standard or reference path length between predator and prey. Here we consider how the ecological neighborhood scales with the environmental properties water clarity (turbidity) and temperature by considering how these properties affect the encounter area and the effective predator density.

The encounter area, or its companion measure, the encounter distance defining the radius of the encounter area, characterizes the ecological neighborhood in which a predation event occurs. Since the reaction distance at which a predator reacts to a prey should be a surrogate for the encounter distance, we can assume α depends on water clarity in the same fashion reaction distance does. Studies show that reaction distance is a function of light level and water clarity (Vogel and Beauchamp 1999). The reaction distance asymptotes with increasing water clarity, so to a first order, for an average light level we express the effect of water clarity on encounter area as

$$\alpha = \alpha_0 \varphi^n \tag{7}$$

where φ is the water clarity expressed as turbidity, which is the distance at which a standard white disk is just detectable by an observer, α_0 is a scaling factor, and n is a coefficient relating how the encounter area increases with water clarity (turbidity). If a predator were able to capture any prey it sees then we could expect $n = 2$, meaning the encounter area would increase as the square of the water clarity. However, because a prey is capable of escaping an attack, the greater the distance of detection the greater is the chance of the prey escaping. Thus, in clear water, a prey should be able to avoid a predator, but when visibility is low and the prey first detects the predator when the two are in close proximity, the chance of escape should be less. These characteristics are represented in Eq. (7) when $n < 2$. Anderson (2003) estimated the reaction area for spring chinook migrating through the tributaries of the Snake River at 9 cm, which is close to the predator reaction distance estimated for similar levels of water clarity.

The ecological neighborhood should also be affected by the predator activity and since activity depends on temperature, we expect the ecological neighborhood is affected by temperature. In fact, predators are strongly affected by water temperature. For example, Vigg et al. (1991) demonstrated that northern pikeminnow’s consumption of smolts, a major prey item, increases significantly with temperature.

Although temperature affects the predation rate, in terms of the XT model it is not clear if temperature affects the encounter area or alters the effective number of predators. Vigg et al. (1991) demonstrated that the number of smolts needed to reach satiation increases with increasing temperature and similarly, the gut evacuation time and the time the animal remains in the satiated state decrease with increasing temperature (Andersen 1999). With these responses, it is possible that at lower temperatures predators satiate more quickly and remain satiated longer so that the fraction of actively foraging predators within a population increases with temperature. Alternatively, temperature may act directly on the encounter area. Since predator activity decreases with temperature, a predator's ability to capture a prey may decrease as its metabolism decreases. Then, as the temperature decreases, the encounter area in which a predator can successfully capture a prey could correspondingly decrease. Leaving aside the mechanisms though which temperature affects predation, for notional convenience, we will assume temperature alters the effective predator density in the habitat and water clarity affects the encounter area.

The effect of temperature on the effective predator density will be described by the parameter equation

8) $$\rho = \rho_0 \theta^m$$

where θ is temperature, m is a shape parameter and ρ_0 is a scaling coefficient. Although Eq.(8) has no upper value and feeding rates as a function of temperature do, Eq.(8) is a suitable representation of the effects of temperature on predator activity up through the range of temperatures that exist in the river environment.

Including Eqs. (7) and (8) into Eq. (5) the survival equation becomes

9) $$S = S_{dam} \exp\left(-\beta \theta^m \varphi^n \sqrt{x^2 + \omega^2 t^2}\right)$$

where

10) $$\beta = \alpha_0 \rho_0 / \delta$$

is a scaling coefficient for the ecological neighborhood.

When $\omega << x/t$ the equation reduces to

11) $$S = S_{dam} \exp\left(-\beta \theta^m \varphi^n x\right)$$

Fitting the model to data

To estimate the model coefficients we begin with Eq.(9) in which dam survival is calculated outside the fitting algorithm according to Eqs.(2) and (3). The equation is rearranged into a multi-linear regression equation

12) $$\left(\log \frac{S}{S_{dam}}\right)^2 = aX^2 + bT^2$$

where the independent regression variables are

13) $$X = \theta^m \varphi^n x \quad \text{and} \quad T = \theta^m \varphi^n t$$

and regression parameters are related to the model coefficients as

14) $$\beta = \sqrt{a} \quad \text{and} \quad \omega = \sqrt{b / a}$$

If the random encounter velocity can be disregarded the regression equation simply reduces to

15) $$\log \frac{S}{S_{dam}} = -\beta X + c$$

where c is a constant to correct for errors in the estimation of the mortality of dam passage.

The model coefficients m, n, β and ω are obtained in a three-step process. First from a matrix of trial values of m and n and arrays of observed temperature, turbidity, travel distance, and travel time X and T regression variable arrays are calculated. Second, for *X* and *T* generated from each *mn* pair coefficients *a* and *b* are obtained from a regression of Eq.(12) or (15) weighted by one over the standard error squared, (1/SE^2). Third, the final values of model coefficients *m* and *n*, along with the best model regression coefficients for *a* and *b,* are selected from the trial regression generating the minimum weighted sum of squares of the model predicted and observed survivals

$$16) \qquad SS = \sum_i \frac{1}{wt_i}\left(S_{obs,i} - S_i\right)^2$$

If a regression with Eq. (12) produces either a negative *b* value, in which the coefficient is not significantly different from zero, or a small positive value then the regression equation reduces to the special case described by Eq. (15).

The choice of how to weight the data results in a tradeoff of factors. Each observed survival estimate has an associated standard error SE derived from the Jolly Sebert method for estimating survival (see Smith et al. 2002). In addition, uncertainties exist in the environmental parameters and the median travel time. Taken together the error estimates are greater for lower survivals over longer reaches than for the estimates over the shorter reaches. However, in many of the release days the number of fish tagged reflects the number of fish passing, which centered about a temperature range representing the average survival. Fewer data for temperatures outside the average are available, so the error in these datasets is greater resulting in higher SE. Including a weighting then biases the regressions towards the average conditions. However, to capture the effect of temperature on survival we require a larger range of temperature and so for this reason it is desirable to emphasize the fewer fish passing under higher temperatures, even though their statistical standard error is greater than in the data representing the majority of fish migrating under average conditions. For the analysis of fish passing through the hydrosystem, sufficient data were available to provide a wide range of temperature and so fish were weighted as $(1/SE)^2$. In the tributaries, however this was not the case and the regressions were not weighted.

Data

The XT model with environmental covariates was applied to PIT data representing the migration of spring/summer chinook, fall chinook, and steelhead over the major segments of the Snake/Columbia River system over the years 1995 to 2002. The fish were tagged with passive integrated transponder (PIT) tags (Prentice, Flagg, and McCutcheon 1990). Releases were divided into run type of wild, hatchery or unknown origin. The data were grouped as daily releases for these species. Release group sizes range between 100 to tens of thousands of fish. The entire data set included over 10,600 individual days of releases. The release sites included tributary release sites, and dam tailraces and forebays. Recapture sites were at downstream dams and survivals thus represented passage over a single reach, which included recapture at the first dam encountered, or over multiple reaches, in which the fish passed through two or more downstream dams.

The environmental parameters representing the average exposure of fish though migration were determined as the averages of the properties over the migration time at the monitoring sites within the reach. The formula is

$$\phi = \frac{1}{N\left(t - t_0\right)} \sum_{n=1}^{N} \sum_{d=t_0}^{t_0+t} \phi_{n,d} \tag{17}$$

where, ϕ is an environmental property, N is the number of monitoring sites, t_0 is the initial day, and t is the travel time to the end of the reach. Exposures were estimated for temperature, turbidity, flow and spill fraction. In addition, the data set contains measures of the total smolt density for each release day. For fish migrating through the hydrosystem, the total smolt density was taken as the passage of all juvenile salmon and steelhead at the release dam on the day of the group's release at the dam. For release groups from the tributaries the smolt density was taken as the total smolt density on the day of median passage at the downstream dam.

Analysis

The XT model characterizes survival in terms of three classes of variables: 1) environmental variables include temperature, turbidity, and travel distance, which are species independent, 2) behavioral variables include the travel time and the random encounter velocity, and 3) ecological variables; β, defining the ecological neighborhood, and *m* and *n,* defining the effect of the environmental variables on the predator-prey interaction.

The question then arises, if the model is a suitable description of the survival dynamics, how specific or generic are the model variables? Clearly, the environmental variables are specific to a particular release. The behavioral variables characterize the movements of predator and prey through their environment. Travel time, or its reciprocal, the average migration speed, depends on the stock and species (Zabel et al 1998, Zabel 2002). The random encounter velocity may depend on species, the stock and the predators. In an ideal simplified sense, we may expect the coefficient *m* is determined by physiological requirements of the predator characterizing its activity with temperature. In this case it may be relatively uniform across the data. In a similar manner, *n* defines how the encounter distance changes with water clarity; ideally, this would be uniform across the data. The factor β is a reciprocal length scale of the ecological neighborhood. It depends on predator density and the encounter area of the predator. We would expect the predator density to be reach specific, while with the base predator density, the scaling factor may be uniform.

In the following sections, the XT based model is applied to the mainstem of the Snake and Columbia Rivers and to the tributaries of the Snake River. The model is applied to chinook and steelhead. In each region, and for each species, the approach is to determine if the model fits the data and then extract model parameters. In assessing the contributions of flow on smolt survival, the random velocity parameter is particularly important, because its value provides a measure of the importance of travel time vs. travel distance on smolt survival. The balance of the two quantitatively assesses the direct importance of flow on smolt survival. In the model, survival is also related to water temperature and water clarity; these factors are quantitatively assessed through the *m* and *n* exponents. Once the model coefficients are estimated it is possible to explore the impacts of the environmental factors on survival to gain a more in-depth evaluation of the possible mechanisms that determine smolt survival. A note of explanation: because the theory used here is entirely new my choice was to present ample examples of the model fits. The essentials of the analysis are summarized and the reader can turn to these sections to extract the main points and conclusions from the analysis.

Survival through the hydrosystem

Chinook survival in the hydrosystem

In this section, the survival of chinook between Lower Granite Dam and McNary dam is evaluated over the years 1995 through 2002. Over 3500 individual days of survival were available over multiple reaches. Survivals include both single and multiple reaches. The single reaches included Lower Granite Dam (LGR) to Little Goose Dam (LGS), LGS to Lower Monumental Dam (LMN). The multiple reaches were LGR to McNary Dam (MCN) and LMN to MCN. In each case, the survival extended from the tailrace of the upper dam to the tailrace of the lower dam. Fish were grouped according to the day of passage at the upper dam resulting in 3528 individual days of survival estimates. The model included all chinook, those migrating in the spring, the summer and the autumn and included both hatchery and wild fish. The survivals estimated in the data were large, ranging from greater than 1.2 to less than 0.05. The numbers released for each day and for each reach were also large, ranging from 10 fish to 180,000 fish in each release. Consequentially, the standard error was large, ranging from 0.001 to 4, with a mean standard error on survival of 0.22. To estimate the model coefficients, first all the data were used in a regression. The parameters for the unweighted fit in Figure 1 are given below.

```
   m    n    β          ω    df   R-sq S(0) Slope
 3.27 0.20 2.77e-007 5.3  3528 0.43 0.25  0.63
```

The terms df, R-sq, S(0) and Slope refer the degrees of freedom, the coefficient of determination, the intercept and the slope in a regression of the model predicted survival against the observed survival shown in the figures. This regression provides a quantitative measure of how well the model fits the data. The temperature coefficient *m* reflects an increase in the mortality rate with temperature and is very close to the rate observed in predator feeding experiments (Vigg et al 1991). The turbidity coefficient *n* is small, suggesting water clarity has a little effect on mortality. The random encounter velocity at 5.3 km/d is small compared to the average migration velocity of 16.5 km/d; noting from Eq.(4) that $\sqrt{16.5^2 + 5.3^2} = 17.37$, is within 5% of the average migration velocity, we may disregard the effects of the encounter velocity and approximate the mortality rate within 5% using Eq.(11) in which survival depends on distance and not migration time.

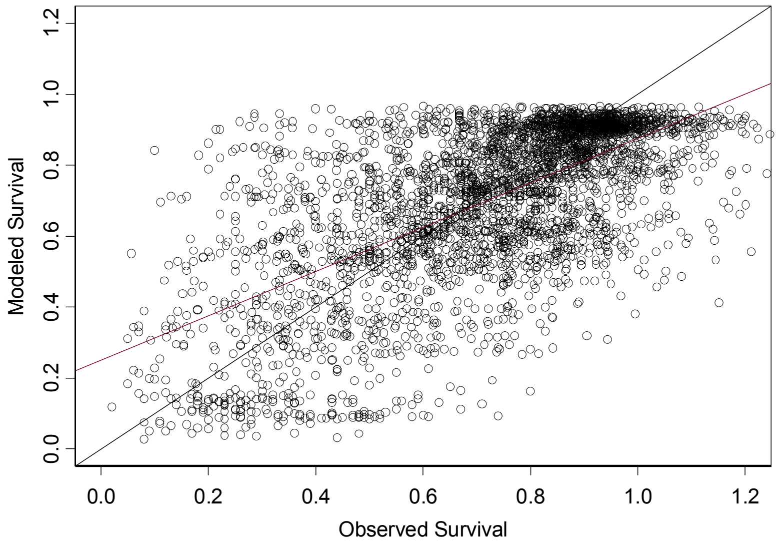

Figure 1. Observed vs. XT-model survival for chinook migration between LGR and MCN dams over the years 1995-2002. Includes all data with weight > 10.

To test the conclusion that the survival could be represented only as a function of distance (X model) the data were regressed using Eq.(15). The resulting regression coefficients are

```
   m n      c     β          df  R-sq S(0) Slope
2.78 0 0.0295   1.91e-006 3528 0.43 0.26  0.61
```

Note the model parameters and fit of the X-model are very similar to the parameters and fit obtained from the XT-model so we conclude the X-model represents the survival processes as well as the XT-model.

Next, the data with large standard errors were removed reducing the data set to 1015 points. The X-model regression for this data is illustrated in Figure 2. The regression coefficients are

```
   m n      c    β        df   R-sq S(0) Slope
3.12 0 0.0312  7.83e-007 1015 0.71 0.13  0.82
```

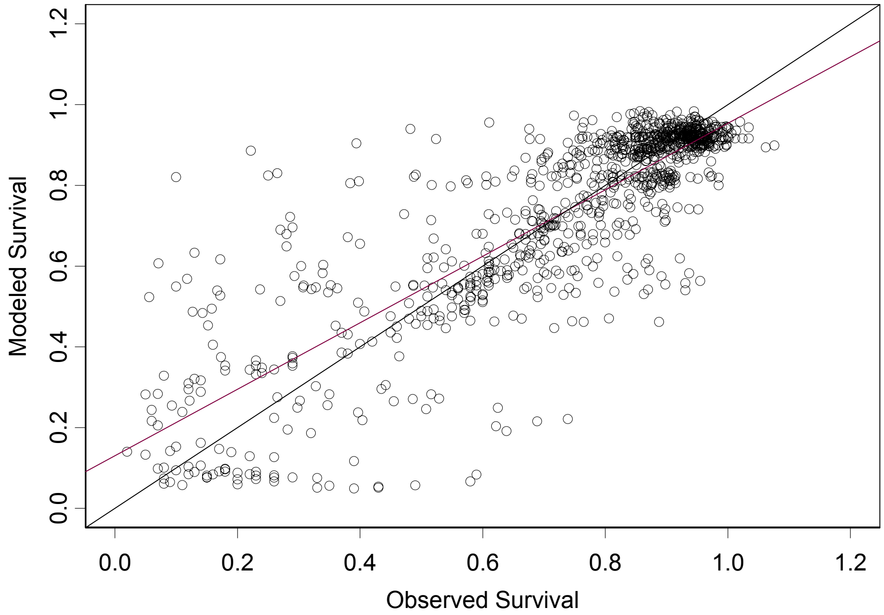

Figure 2. Observed vs. X-model survival for chinook migration between LGR and MCN over the years 1995-2002. Includes all data with weight > 200.

In theory, the parameters *m* and *n* are expected to be essentially invariant if they reflect ecological processes. Therefore, if the model can suitably represent survival it should do a reasonable job of fitting different years with the same *m* and *n* values. However, because the predator population itself varies between years, we expect the β coefficient to be different between years. Figure 3 through Figure 5 demonstrate the X-model fit by varying β only. Figure 3 represents a typical year 2002, Figure 4 represents an extremely low flow year, 2001, and Figure 5 represents an extremely high flow year, 1997. The figures show that the model fits well both the very low flow year and the average flow year. It does not fit the 1997, high flow year, and we note that in this year the XT-model gives a large ω, so that chinook survival was anomalously dependent on travel time as well as distance.

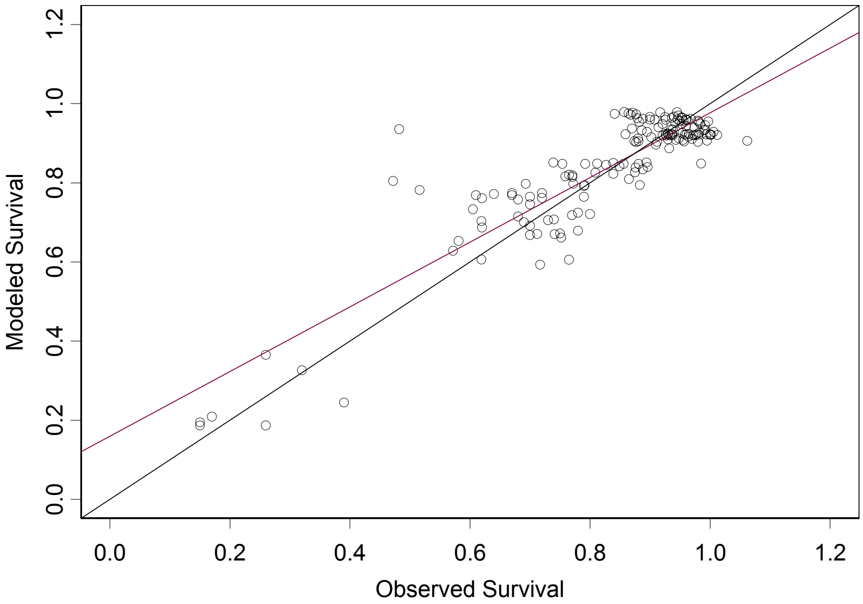

Figure 3 Observed vs. X-model survival for chinook migration between LGR and MCN dams in 2002. Includes all data with weight > 200.

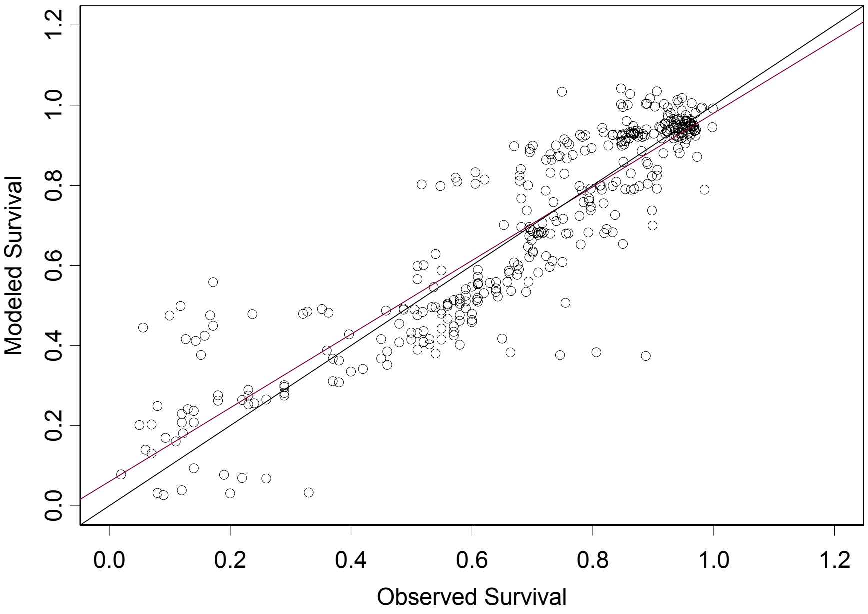

Figure 4 Observed vs. X-model survival for chinook migration between LGR and MCN dams in 2001. Includes all data with weight > 200.

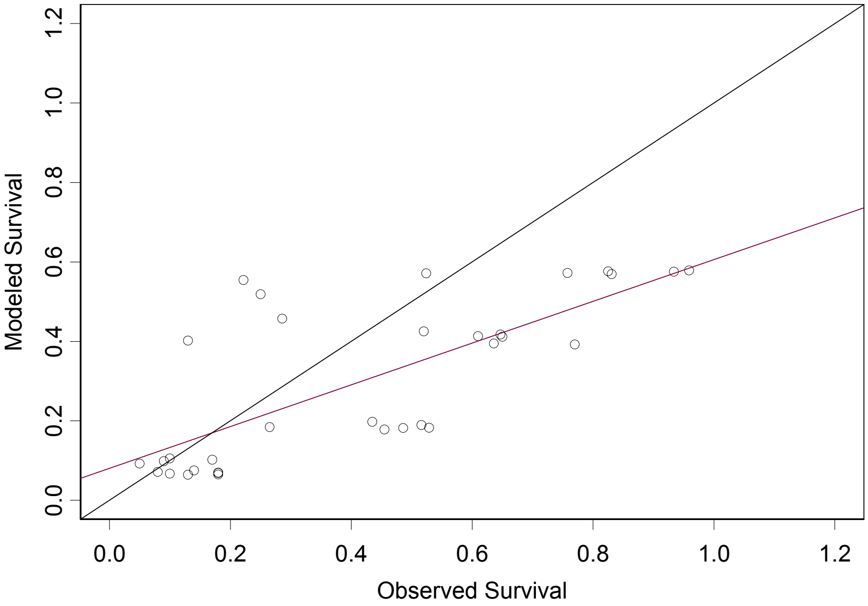

Figure 5. Observed vs. X-model survival for chinook migration between LGR and MCN dams in 1997. Includes all data with weight > 200.

Individual years fits using *m* and *n* derived from all years together are compared fits in which *m* and *n* are estimated for each year is illustrated in Table 1. In general, the model fit improves slightly when the model is allowed to adjust *m* and *n* as well as β. However, the standard deviation of β is considerably less under the fixed *mn* regression (2.7e-07) than with the variable *mn* regression (3.4 e-03), while the average R-squares are very similar: 0.69 for fixed *mn* regression and 0.73 for the variable *mn* regression. From this, we may conclude that the penalty for using fixed *m* and *n* in terms of fitting the data is slight, and the benefit is a significantly lower standard deviation on the β term. Considering that the ecological foundations of the equation, a fixed *mn,* and lower β variability between years, X-model is more realistic. Furthermore, the fixed *m* value corresponds to the laboratory observed temperature response of predators as measured by Vigg et al (1991).

Table 1. Comparison of fit with fixed *mn* vs. variable *mn* for LGR to MCN using the X-model with wt = 200. S(0) and Slope are the intercept and slope of the regression of the modeled vs. observed survival, R-sq is the coefficient of determination and df is the degrees of freedom.

	Year	**m**	**n**	**β**	**df**	**R-sq**	**S(0)**	**Slope**
Fixed *mn*	1995	3.12	0	5.79E-07	103	0.64	0.3	0.54
	1996	3.12	0	3.03E-07	22	0.73	0.22	0.43
	1997	3.12	0	7.35E-07	31	0.54	0.08	0.53
	1998	3.12	0	2.45E-07	103	0.72	0.16	0.77
	1999	3.12	0	8.02E-07	159	0.78	0.16	0.8
	2000	3.12	0	5.76E-07	47	0.52	0.4	0.48
	2001	3.12	0	1.07E-06	378	0.81	0.06	0.92
	2002	3.12	0	4.80E-07	158	0.8	0.16	0.82
	all years	3.12	0	7.72E-07	1015	0.71	0.13	0.82
Varaible *mn*	1995	0.62	0.12	9.64E-04	103	0.72	0.25	0.65
	1996	0	0.12	4.97E-03	22	0.79	0.2	0.54
	1997	0	0.12	9.12E-03	31	0.65	0.06	0.79
	1998	1.25	2.5	3.00E-06	103	0.77	0.12	0.82
	1999	3.75	0	1.21E-07	159	0.78	0.19	0.77
	2000	4.38	0	1.29E-08	47	0.52	0.4	0.47
	2001	4.38	0	2.76E-08	378	0.82	0.12	0.84
	2002	2.5	0	3.15E-06	158	0.8	0.13	0.85
	all years	3.12	0	7.72E-07	1015	0.71	0.13	0.82

Survival and environmental conditions

Figure 6 through Figure 8 explore how the observed and modeled survivals relate to environmental conditions over the seven years of studies. In the figures, the model survivals were generated using migration distance and temperature plus the model parameters m and β,, which were fixed for all reaches, years and release days. Also, because the fit for all years gave $n = 0$, turbidity was not included in the model. A significant amount of information is contained in these graphs. Each PIT tag estimated survival (observed) has a corresponding X-model generated survival (modeled). The two share the same x-axis position, corresponding to the environmental variable value, and the degree of separation on the y-axis corresponds to differences between observed and modeled survivals. The observed survival contains observational error and the modeled survival contains parameter estimation error and process error, not captured by the X model. Both the observed and modeled points share the same environmental parameter value, which contains observation error. Both the observed and modeled survivals exhibit patterns with the environmental variable and the correspondence between the patterns provides a qualitative description of the importance of the environmental variable to the data and the model. A random pattern in both observed and modeled survivals suggests the environmental parameter is not significant in determining survival. A nonrandom pattern in observed survivals and a random pattern in the modeled survivals suggests the model is missing a factor, and a pattern in the model that is not found in the observations may suggest the model erroneously represents a pattern, or the observations contained significant error covering up the pattern.

Figure 6 shows observed and modeled survivals over the day of the year. The various coherent lines of model survivals represent different years and river reaches. Generally, the higher lines correspond to the shorter reaches and the lower lines correspond to the longer reaches. The observed survivals and modeled survivals follow similar trends, decreasing over the year as first the spring migrants pass through the system and later, as the summer migrants pass through the system. Notice the observed survivals exhibit greater variation in the summer period.

Typically, fewer fish are tagged during the summer and the standard errors on their survival estimates are higher.

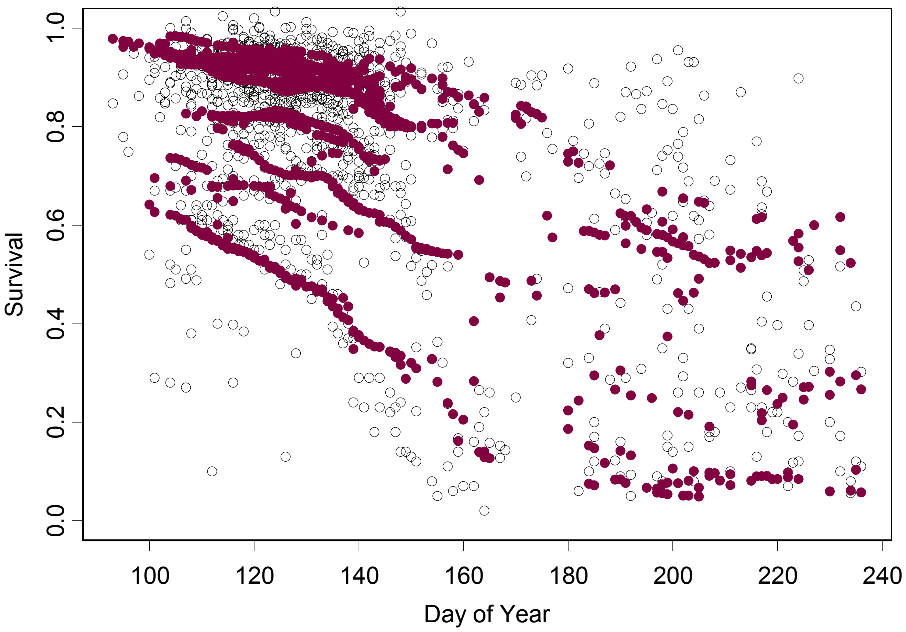

Figure 6. Modeled and observed chinook survival vs. day of the year over single and multiple reaches between LGR to MCN over the years 1995-2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

Figure 7 shows how survival varies with temperature. Notice that both the observed and modeled survivals decline with increasing temperature. The variability with temperature is less for the spring observed survivals than for the summer survivals. The three groups of modeled survival correspond to fish passing one two or three dams. The pattern in the modeled survivals is also observed in the data.

Figure 8 shows that the observed and modeled survivals exhibit similar patterns with travel time, with high survivals associated with short travel times over the shorter reaches. Intermediate survivals (0.4-0.6) over a range of travel times are found in both the model and the data. The low survivals over a range of travel times occur for both the model and the observations. Note that while the model pattern is very similar to the observed pattern, the model does not contain travel time. In effect, the travel time element is captured by the X dependence of the model.

Figure 9 shows the observed and modeled survivals exhibit similar high variability with flow. Both exhibit a group of high survivals with variable flows, as represented by the elongated cloud of points for survivals above 0.8. Both the model and observed survivals have a group of low survivals at low flows. In the model these are produced by the higher temperatures associated with the low flows that occur in the summer in all years and the throughout all of 2001.

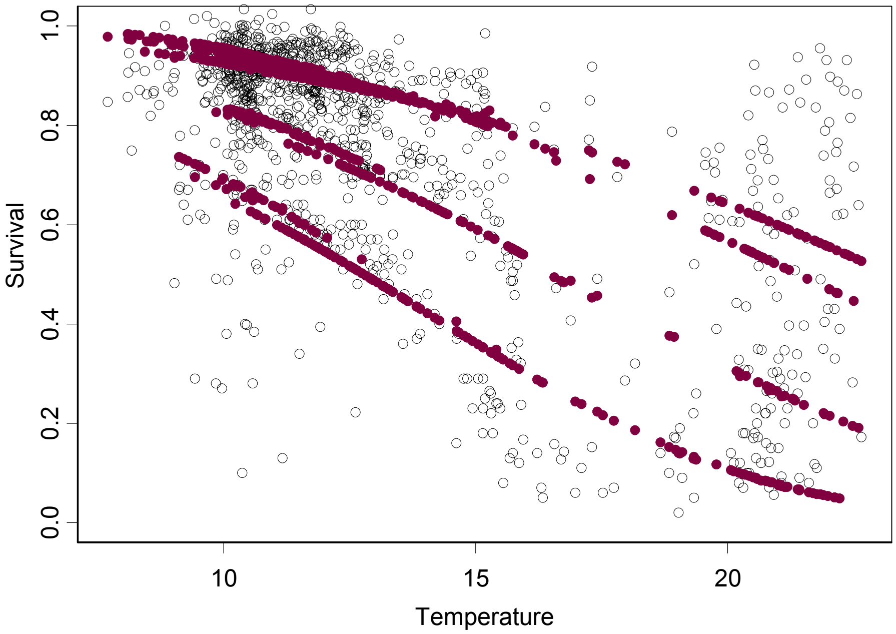

Figure 7. Modeled and observed chinook survival vs. temperature (^oC) over single and multiple reaches between LGR to MCN over the years 1995-2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

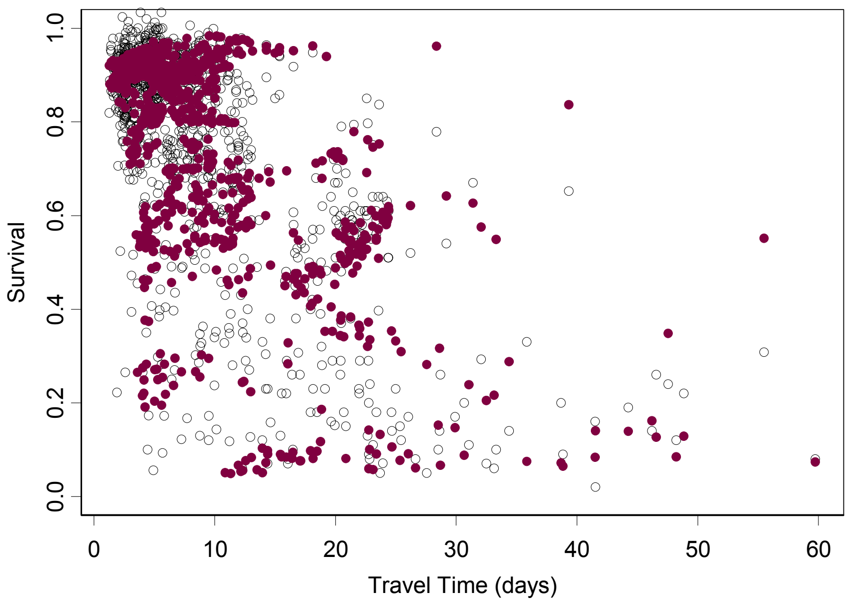

Figure 8. Modeled and observed chinook survival vs. travel time over single and multiple reaches between LGR to MCN over the years 1995-2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

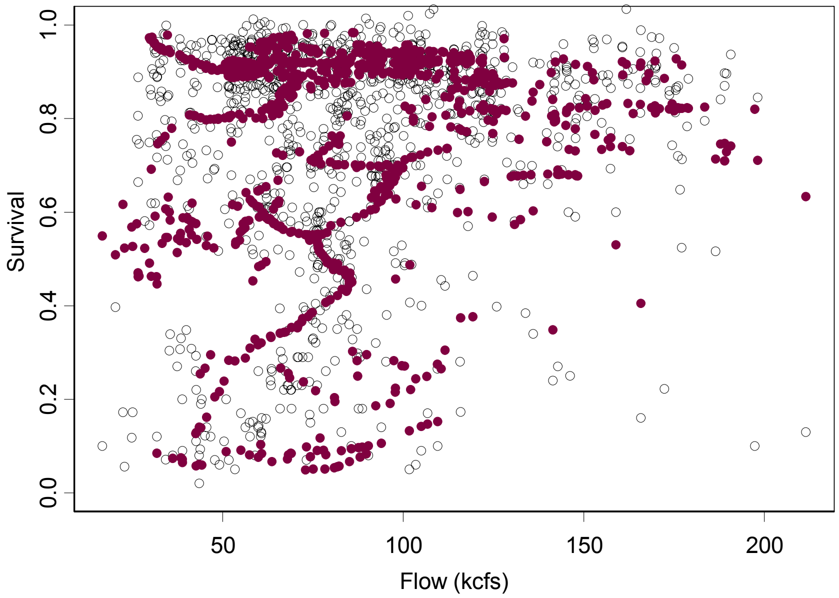

Figure 9. Modeled and observed chinook survival vs. flow over single and multiple reaches between LGR to MCN over the years 1995-2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

Comparison with 2001

The above figures provide a qualitative illustration of how well the model, with two variables and two parameters, reproduces the observed patterns between the environmental parameters and survival. Figure 10 through Figure 14 explore the correspondence in more detail using data over a single reach (LGR to MCN) for a single year 2001. This data is particularly illustrative because 2001 was a year of anomalously low flow and low survivals for which there were a larger number of high quality survival observations. Thus, the data is a good test of the model since the data is of high quality and anomalous. In the figures the temperature coefficient was set at its fixed value (derived across years) of 3.14 and β was derived for the regression for 2001 year (Table 1), which was within one standard deviation of the mean value for the coefficient obtained by fitting all years.

Figure 10 illustrates the X-model survival tracks very well the observed trend in survival over the period from March through July. Because the reach length is fixed, only temperature determines survival in this example.

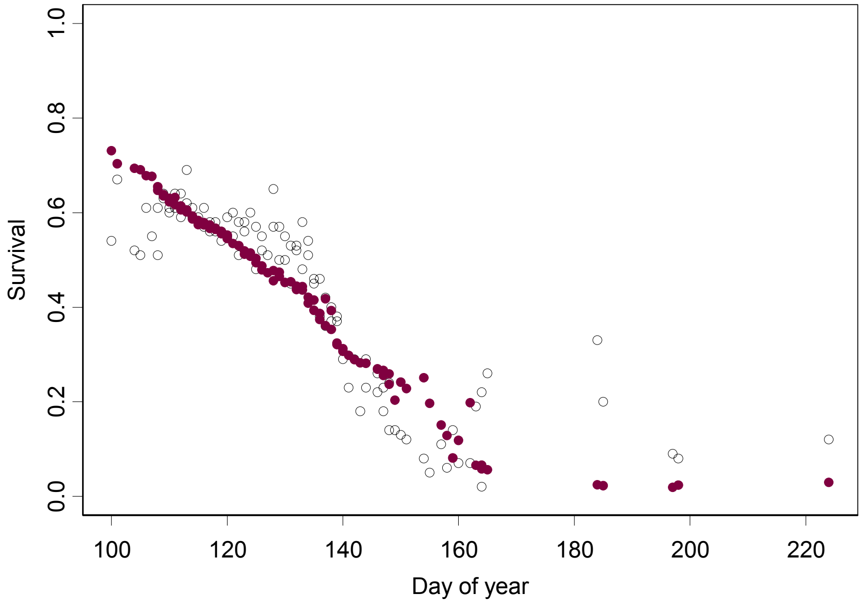

Figure 10. Modeled and observed chinook survival vs. day of the year for migration between LGR and MCN in 2001. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

Figure 11 shows the model and observed survivals against turbidity, which is a measure of the water clarity. Again the model tracks very well the observed pattern and does so with the turbidity exponent of $n = 0$. That is, the model regression indicated that all the patterns in survival could be captured through variations in temperature. The pattern with turbidity then results through the seasonal correlation between turbidity and temperature.

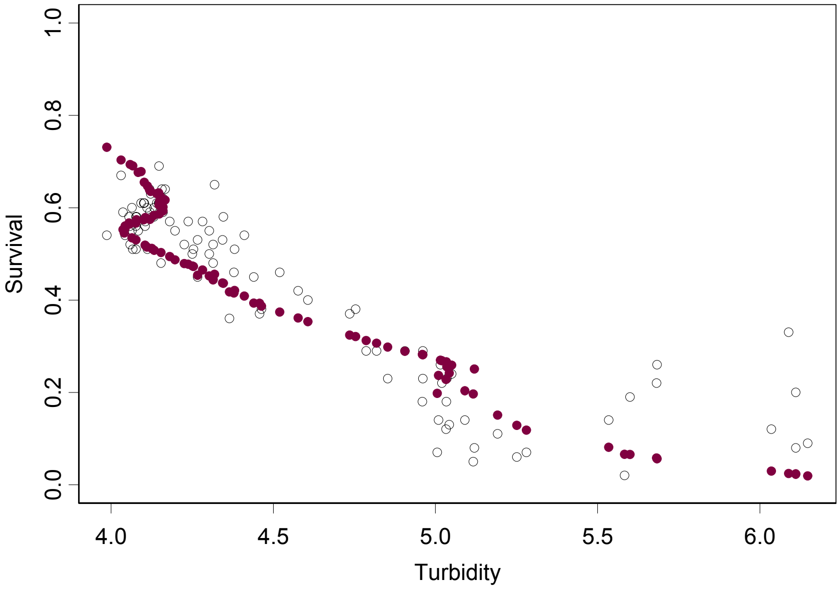

Figure 11. Modeled and observed chinook survival vs. turbidity (ft) for migration between LGR and MCN in 2001. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

Figure 12 shows the model and observed survivals against temperature. Note this correspondence was obtained with the m value fit using all years and all reaches and the β parameter was fit for the year 2001 and all reaches. However, the correspondence between the model and observations is good. A better fit could be obtained using a more physiologically based model to describe the effect of temperature on predators and by fitting the model to the specific survivals over the reach. However, the intent here is to demonstrate that survivals in this anomalously warm year as well as in a normal year can be generated with temperature only.

During the 2001 spring migration, the temperatures were about two degrees warmer than in the other years of the data set.

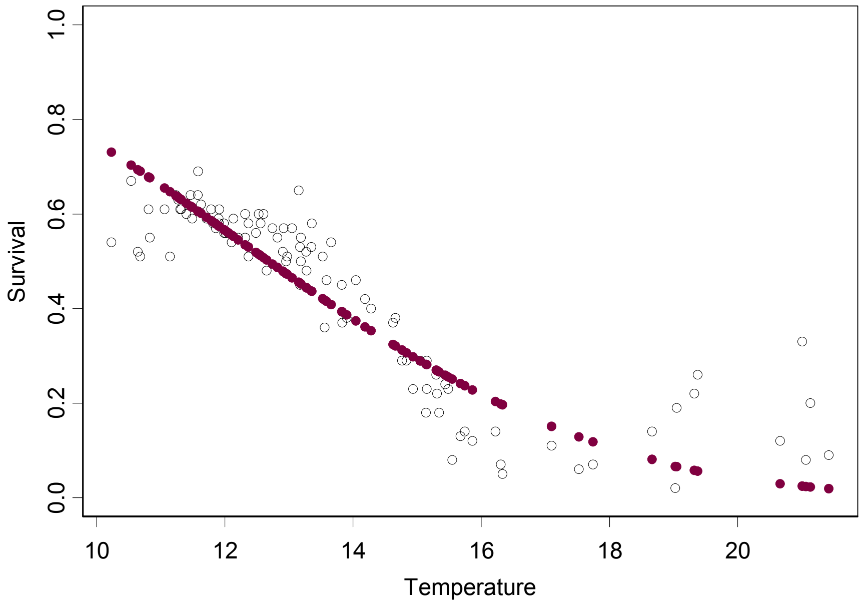

Figure 12. Modeled and observed chinook survival vs. temperature (^{o}C) for migration between LGR and MCN in 2001. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

Figure 13 shows the model and observed survivals against travel time. The model fits the observed pattern with survival both increasing and decreasing with travel time indicating that travel time is not a significant factor in determining survival over this reach in 2001.

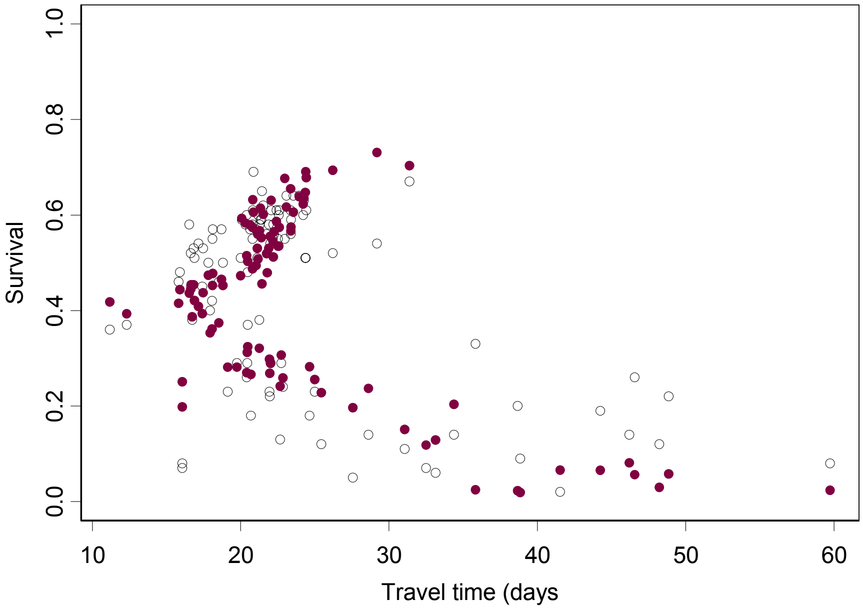

Figure 13. Modeled and observed chinook survival vs. travel time for migration between LGR and MCN in 2001. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

A similar pattern is exhibited with flow and the model fits the pattern well (Figure 14). Here survival continually decreases over the season as the water warms but the flow follows a different pattern, increasing up to the spring maximum flow and then decreasing into the summer resulting in a > shape. This clearly demonstrates flow is decoupled from survival within the season. The model captures this relationship very well and at the same time captures the year-to-year variation in survival, which is explained by year-to-year variations in temperature and predator activity that increases as a power function of temperature. In effect, as demonstrated in laboratory experiments, survival data and the model, predator foraging is strongly dependent on temperature and the incremental increase per unit of temperature is greater as the temperature increases. In effect, temperature accelerates mortality and that is all that is required to explain both the within season pattern and the between year pattern of survival for chinook.

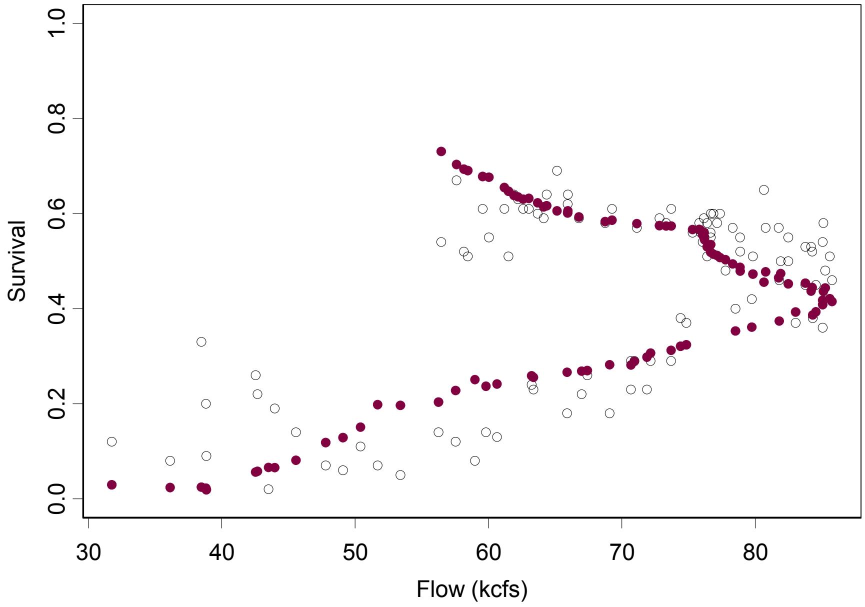

Figure 14. Modeled and observed chinook survival vs. flow for migration between LGR and MCN in 2001. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

Steelhead analysis

An XT-model analysis for steelhead reveals similar results to those found for chinook. However, in the case of steelhead, the analysis indicates that the random encounter velocity is essentially zero and the best model fit for the steelhead survival between LGR and MCN dams is obtained only with the X-model. The XT-model does not fit that data as well. A regression of all available data is illustrated in Figure 15. The X-model coefficients below are similar to those found for chinook. Also shown are the coefficients for the linear regression between the model and observed survivals and weights 10 and 200.

wt	m	n	β	df	R-sq	S(0)	Slope
10	2.78	0.11	6.46e-006	1185	0.47	0.09	0.75
200	2.22	0.11	3.08e-005	315	0.82	-0.02	0.99

Note in Figure 16 the 2001 results (solid dots) are not anomalous to other years. This was an extremely low flow year with low steelhead survivals through MCN reservoir. However, model was able to fit this data with temperature only.

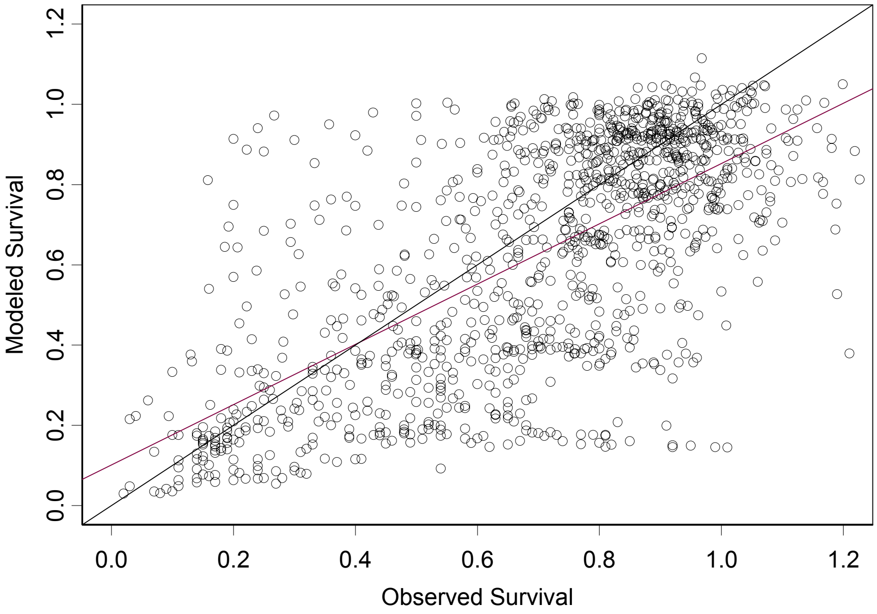

Figure 15. Observed vs. X-model survival for steelhead migration between LGR and MCN dams over the years 1995-2002 based on 1185 data points with a weighting factor > 10.

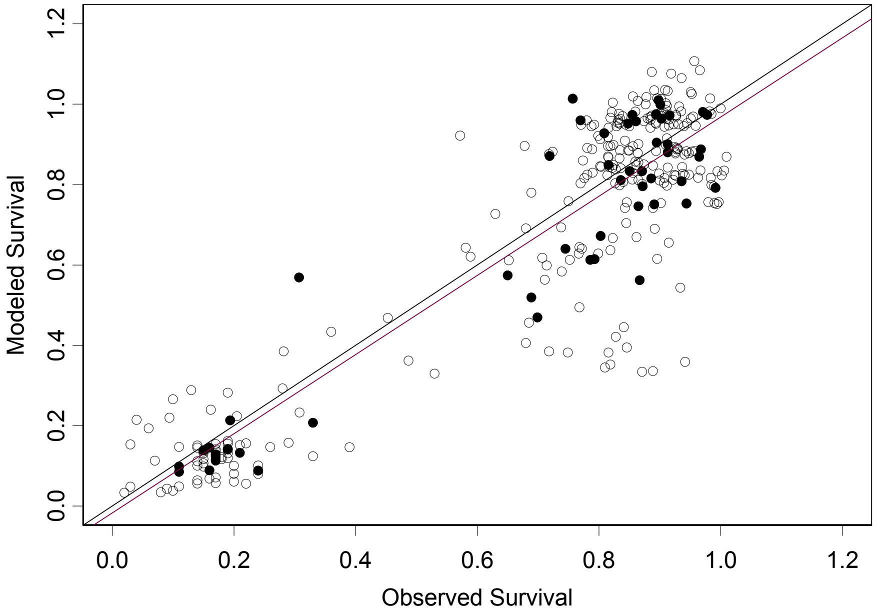

Figure 16. Observed vs. X-model survival for steelhead migration between LGR and MCN dams over the years 1995-2002 based on 315 data points with a weighting > 200. The solid dots represent 2001 data.

Survival through Snake River tributaries

Snake River spring chinook

Snake River spring chinook released from multiple hatcheries beginning in 1993 show survival to Lower Granite Dam is a function of distance from the hatchery to the dam (Muir et al. 2001). Anderson and Zabel (Anderson 2003) fit the XT-model without temperature or turbidity to data from 1993 to 1998 and obtained a random encounter velocity of $\omega = 9.5$ km/d. However, in individual years, the XT-model did not fit the data well and the X-model better represented the data.

To explore the factors that determine survival in these fish the XT-model including temperature and turbidity was applied. For these fish, the data was unweighted. This choice was made because the numbers of releases of fish from the further upstream hatcheries was considerably less and weighting by the standard error unduly emphases the hatcheries nearer Lower Granite Dam. Again, the model was able to fit some of the years, with $\omega > 0$ while in other years the X-model was required. Fitting the XT-model to the combined years 1995-2002 produced trends in plots of survival residuals vs. environmental parameters while the fit of the X-model did not. Therefore, as observed by Muir et al (2001), survival of these fish seems best represented as a function of distance. Furthermore, the X-model analysis also indicated neither temperature nor turbidity had any effect on survival. The resulting model coefficients are given below.

m	n	β	df	R-sq	S(0)	Slope
0	0.00	0.001383	400	0.39	0.43	0.41

The modeled survival fit to the observed survivals follows the general one-to-one trend line (Figure 17). There is considerable scatter about the line, which cannot be explained by temperature or turbidity. However, the fish in this data set are from distinct hatcheries with very different rearing histories and with each release group traveling through its unique tributary pathway. These factors undeniably contribute to systematic differences in the release groups, which can account for the high variability in the plot of the modeled vs. observed survivals. In contrast, the fish from the hydrosystem analysis had different histories but experienced the same environment in the hydrosystem. Thus, we would not expect a strong fit using a single β value and distance to represent survivals of all fish from the hatcheries over all years. However, when the X-model was applied to data from individual years the fit was significantly better as is illustrated in (Figure 18).

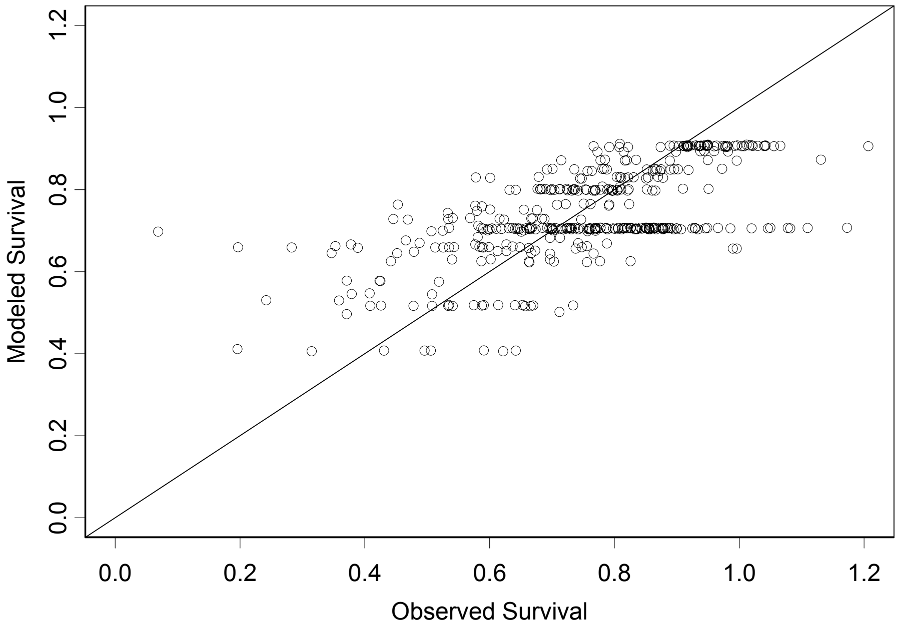

Figure 17. Observed vs. X-model survival for hatchery spring chinook migration between the hatchery release points and LGR Dam over the years 1995-2002 based on 400 data points with no weighting.

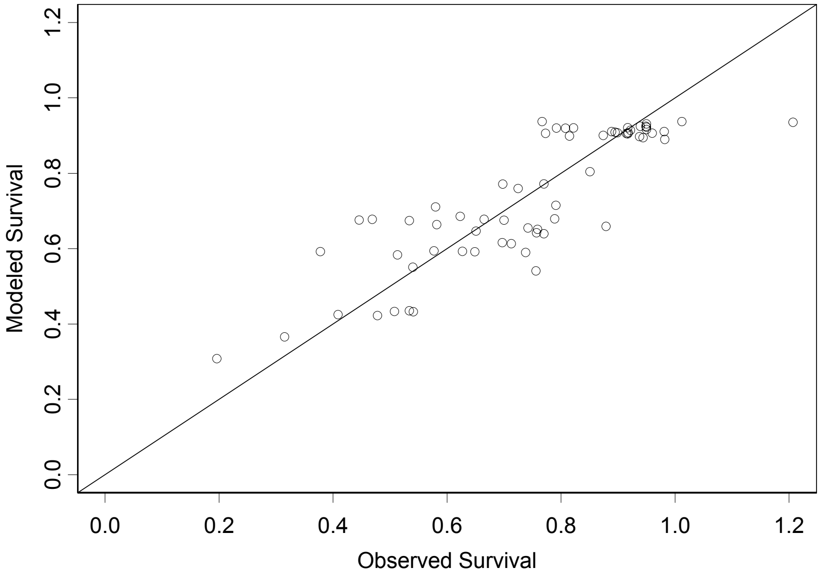

Figure 18. Observed vs. X-model survival for hatchery spring chinook migration between the hatchery release points and LGR Dam for 1995 based on 62 data points with no weighting.

Snake River spring chinook and environmental properties

The pattern of survival with environmental properties shows the simple X-dependent relationship of survival in these fish (Figure 19). The pattern of survival with migration distance is clear although the variability about the trend is large for possible reasons discussed above. A pattern does also exist between survival and travel time, but in terms of the model this is an artifact: travel time is generally longer for fish that migrate longer distances (Figure 20). As Muir et al (2001) illustrated and as can be demonstrated by the data, fitting survival cannot be explained through a regression with travel time. The data exhibits a positive trend between survival and flow (Figure 21) with the lowest survivals below 50 kcfs flow at LGR dam and the highest survivals at flows above 100 kcfs. The same trend emerges from the X-model, but because survival depends only on distance traveled and has no flow effect whatsoever, we surmise that the flow trend is a result of the fish traveling shorter distances were released during higher flows. The possibility of such a spurious correlation serves to illustrate the problems with extracting mechanisms from regression approaches exclusively. Finally, the observed survival data does not exhibit a trend with temperature (Figure 22). Consequentially the X-model fit gave *m* = 0 and as illustrated in the figure the model has no survival-temperature relationship.

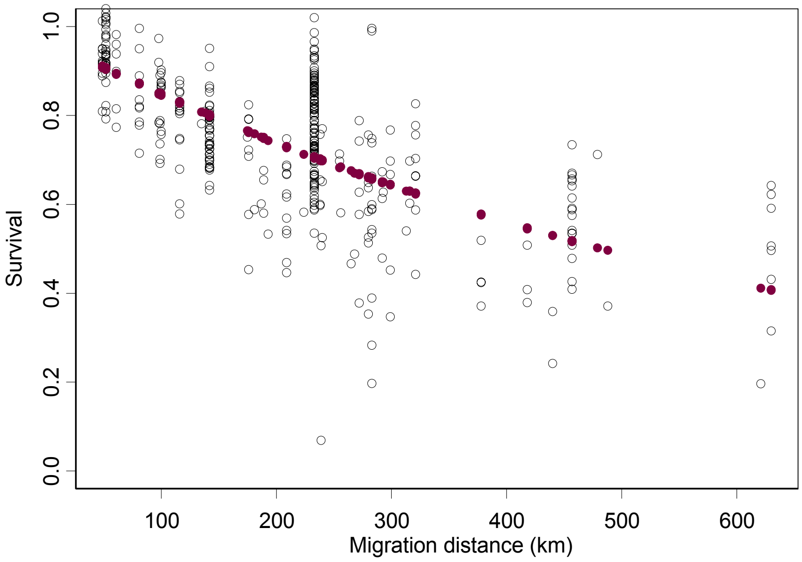

Figure 19. Modeled and observed Snake River spring chinook survival vs. travel distance for migration from hatcheries release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

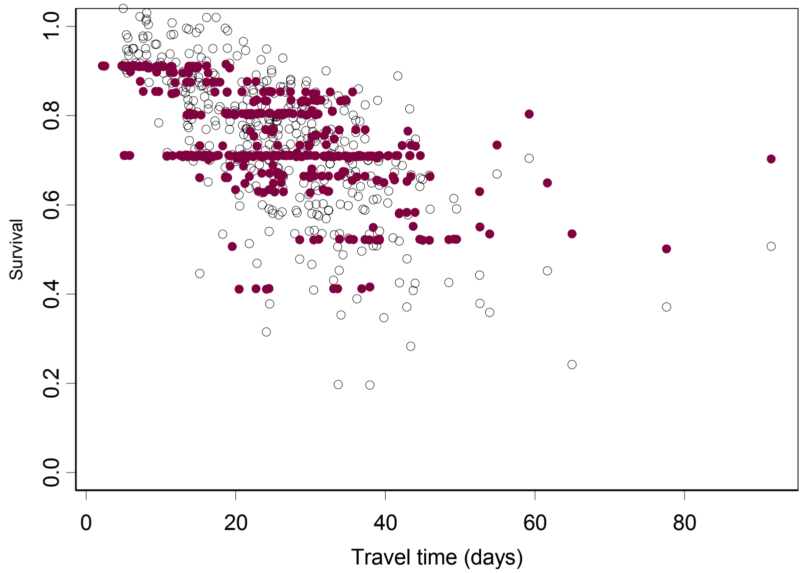

Figure 20. Modeled and observed Snake River spring chinook survival vs. travel time for migration from hatcheries release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

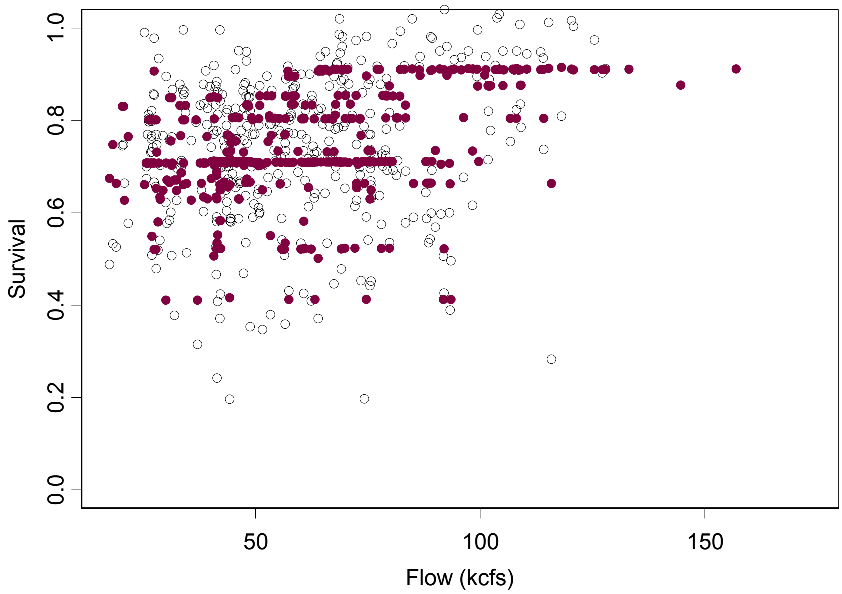

Figure 21. Modeled and observed Snake River spring chinook survival vs. flow for migration from hatcheries release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

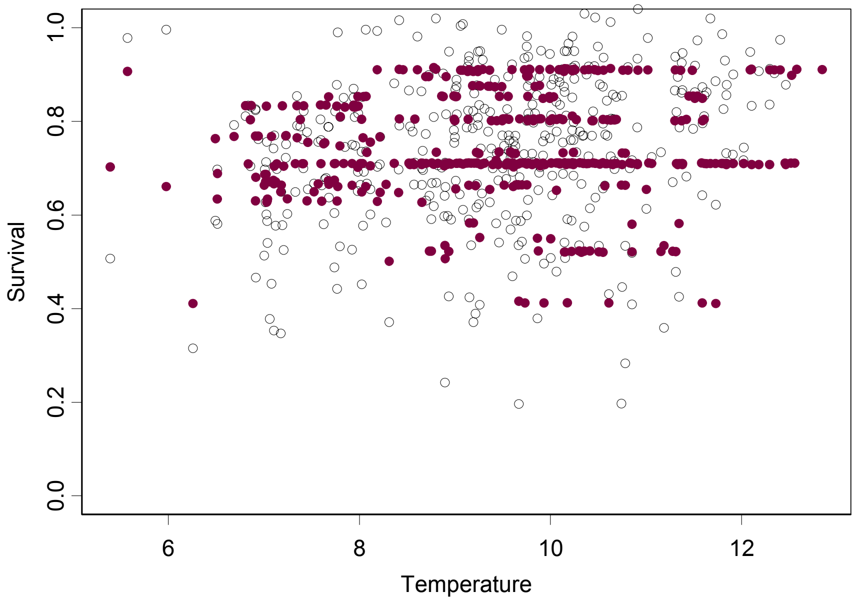

Figure 22. Modeled and observed Snake River spring chinook survival vs. temperature (^{o}C) for migration from hatchery release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

Snake River fall chinook

The XT model fit the Snake River fall chinook data well. In this case, the data were unweighted but the standard error was similar for each release day and variations in weighting had no significant impact on the estimation of the model parameters. The estimated parameters and the fit of the observed and modeled survivals are given below. Again, the *m* coefficient is similar to that found for chinook and steelhead in the hydrosystem,

```
   m    n       b     w   df R-sq  S(0) Slope
2.96 1.04 3.69e-007 1.7 225 0.68  0.10  0.78
```

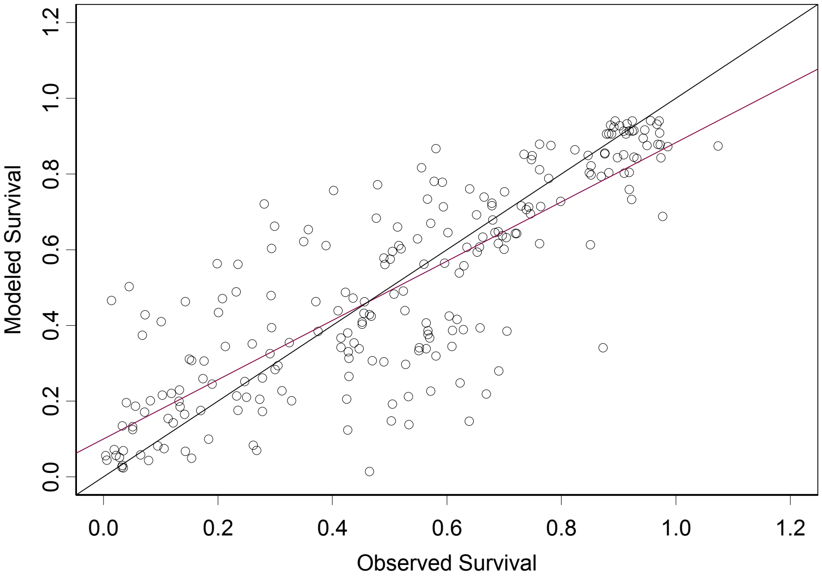

Figure 23. Observed vs. X-model survival for hatchery fall chinook migration between the Snake River release points and LGR Dam over the years 1995-2002 based on 227 data points with no weighting.

Correlations with environmental properties

Fall chinook exhibit interesting patterns with the environmental parameters, which are reflected in all model coefficients being significant and non-zero. Correlations for day of the year, temperature, turbidity, travel time, LGR spill fraction, and flow all show significant patterns, which are well represented by the XT-model Figure 24 to Figure 29. This represents one of the most interesting datasets available and demonstrates that all processes can combine to determine fish survival. The good correlations and the well-defined patterns serve to illustrate that in some cases factors interact.

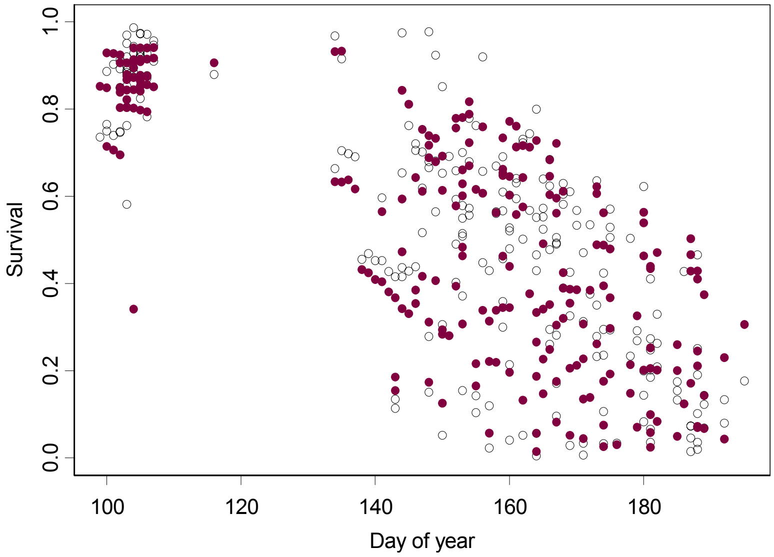

Figure 24. Modeled and observed Snake River fall chinook survival vs. day of the year for migration from Snake River release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

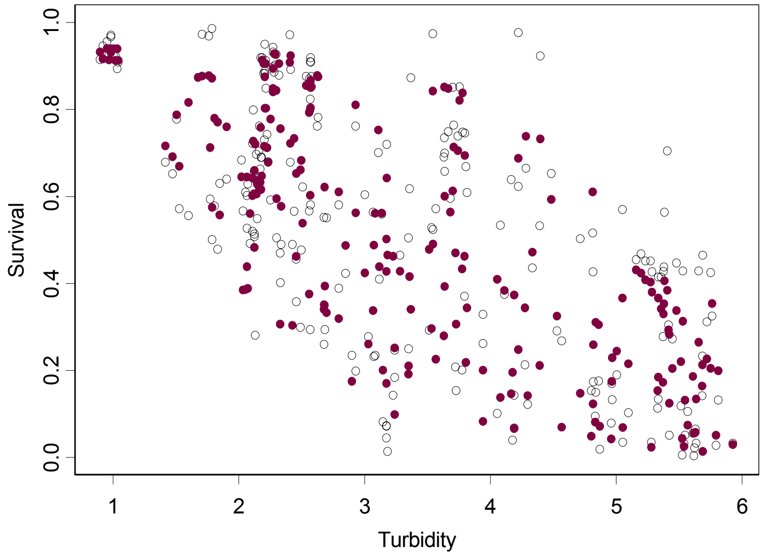

Figure 25. Modeled and observed Snake River fall chinook survival vs. turbidity (ft) for migration from Snake River release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

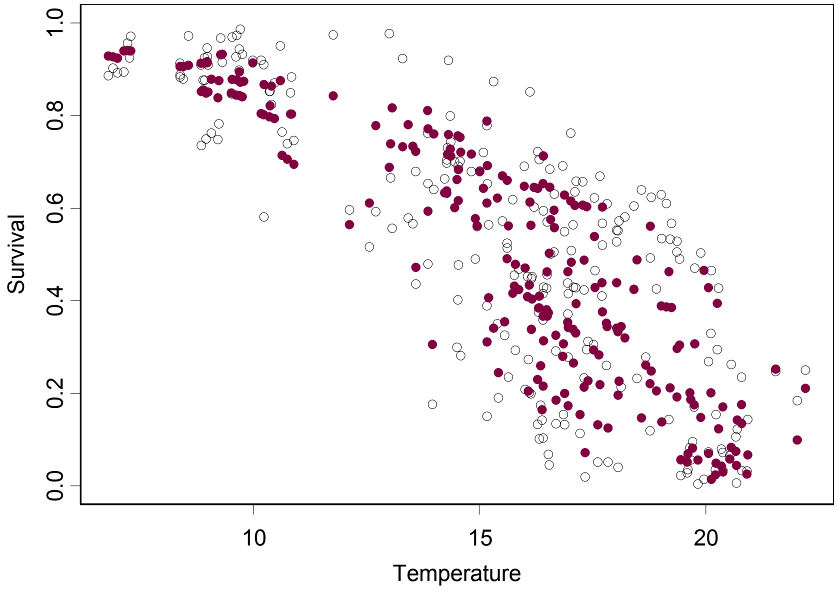

Figure 26. Modeled and observed Snake River fall chinook survival vs. temperature (^{o}C) for migration from Snake River release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

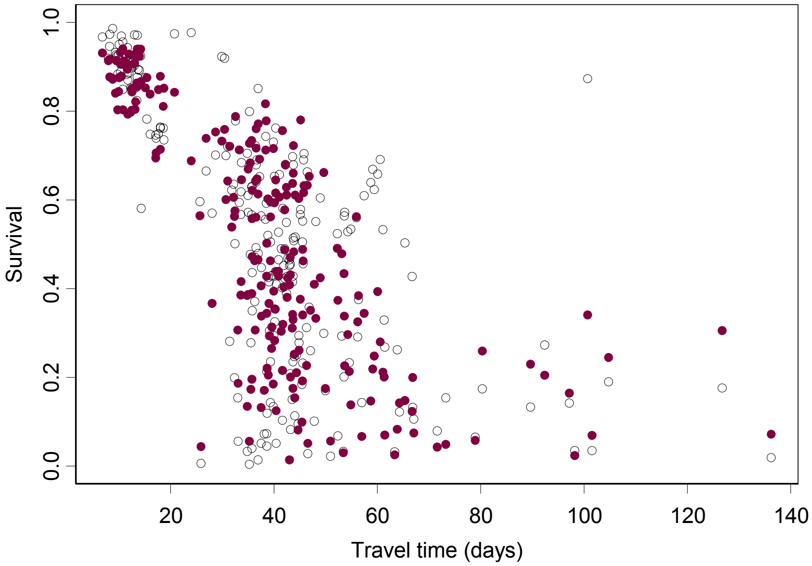

Figure 27. Modeled and observed Snake River fall chinook survival vs. travel time for migration from Snake River release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

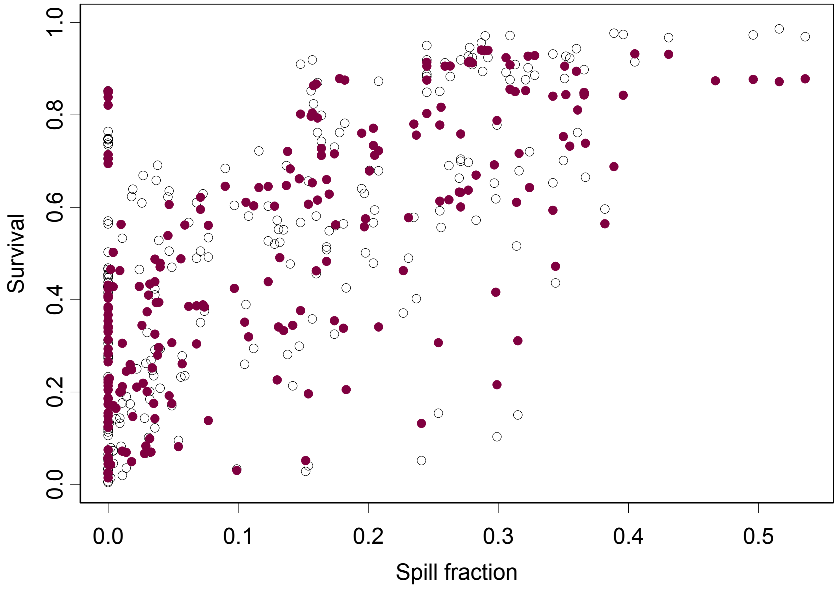

Figure 28. Modeled and observed Snake River fall chinook survival vs. LGR spill fraction for migration from Snake River release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

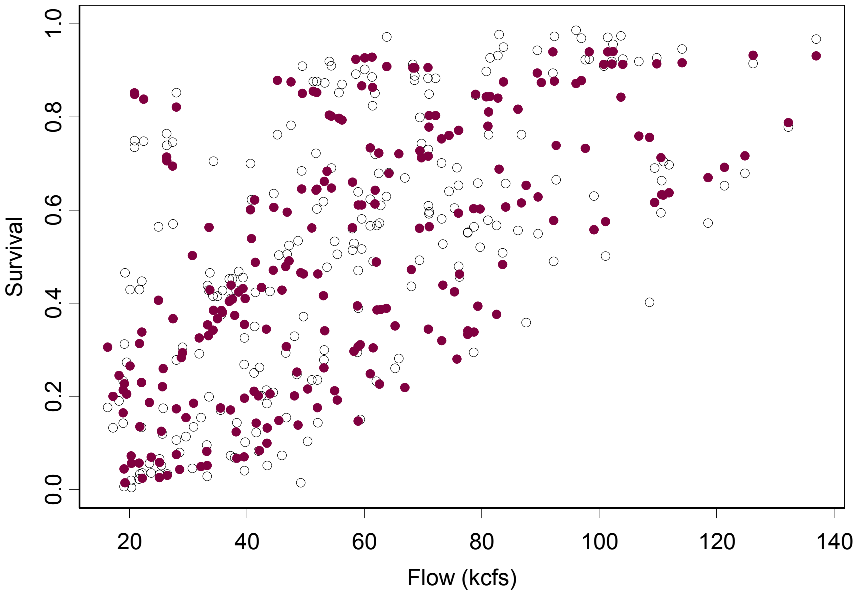

Figure 29. Modeled and observed Snake River fall chinook survival vs. flow for migration from Snake River release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

Snake River steelhead

Snake River steelhead chinook released from multiple hatcheries between 1995 and 2002 were best fit by the XT-model suggesting that survival was dependent on both distance traveled and travel time in this stock. However, like the spring chinook, neither temperature nor turbidity variations correlated with survival. The estimated parameters and the fit of the observed and modeled survivals are given below.

```
  m    n       β      ω   df  R-sq S(0) Slope
 0     0 0.0008180 19.7 553 0.37 0.34  0.53
```

In the fit, unweighted data were used and, as with the spring chinook, the correlation between observed and modeled survivals exhibited significant variation (Figure 30). Again, as with the spring chinook, the fish were released from different hatcheries and traveled through unique tributaries prior to the common collection at LGR Dam. Therefore, these fish, as with the spring chinook, exhibited the least similarity between release and recapture and it is not surprising that model fit has greater variation.

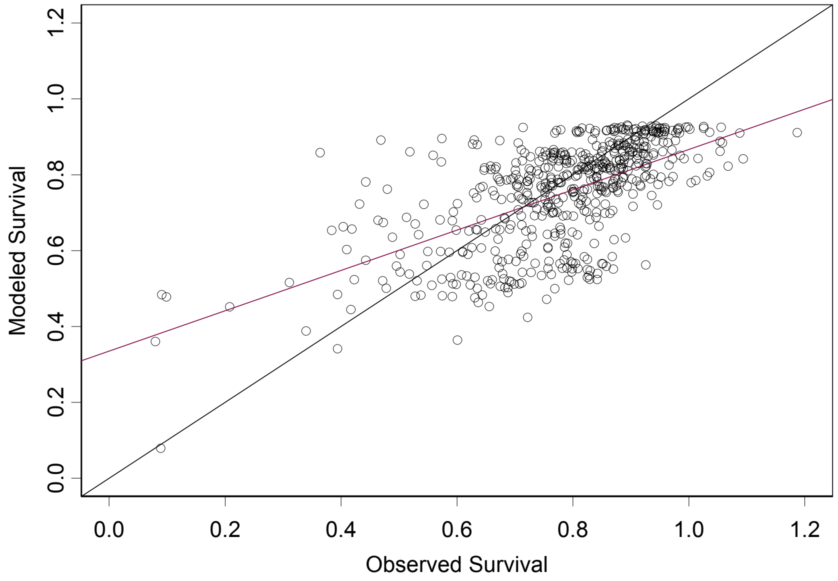

Figure 30. Observed vs. X-model survival for hatchery steelhead migration between the hatchery release points and LGR Dam over the years 1995-2002 based on 555 data points with no weighting.

Correlation with environmental properties

Snake River steelhead survival exhibited a weak relationship between survival and day of the year, suggesting an insignificant seasonal trend in their survival through the tributaries (Figure 31). However, survival was correlated with travel distance (Figure 32) and travel time (Figure 34) but not with temperature (Figure 33) or turbidity. The survival exhibited no significant pattern with flow (Figure 35). Correspondingly, during early migration the travel time of these fish, like that in other species, is independent of water flow (Zabel 2002). Therefore, a lack of correlation with flow but a correlation with travel time is expected.

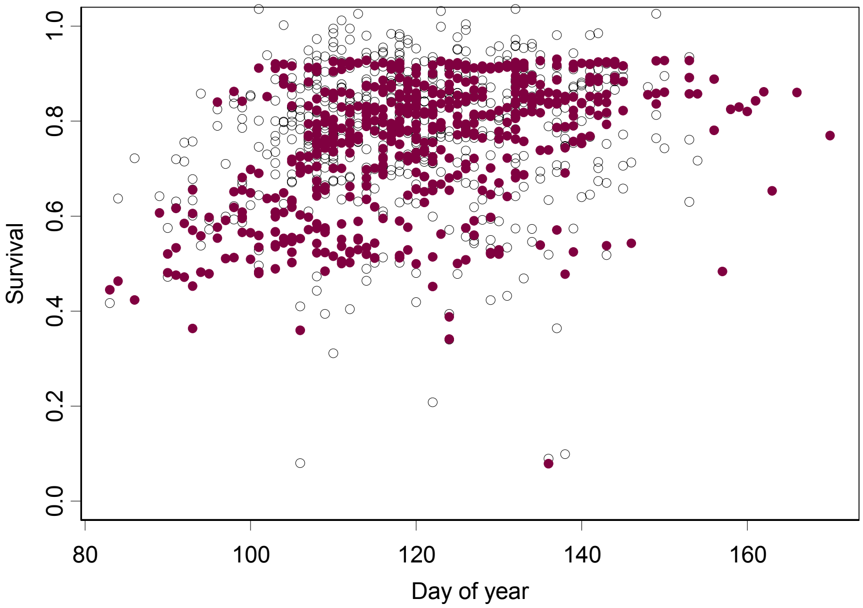

Figure 31. Modeled and observed Snake River steelhead survival vs. day of year for migration from Snake River hatchery release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

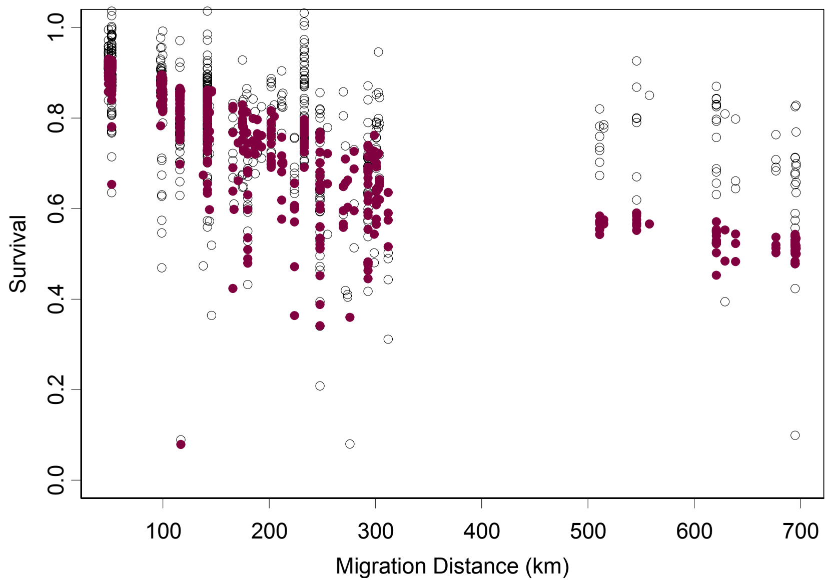

Figure 32. Modeled and observed Snake River steelhead survival vs. migration distance for migration from Snake River hatchery release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

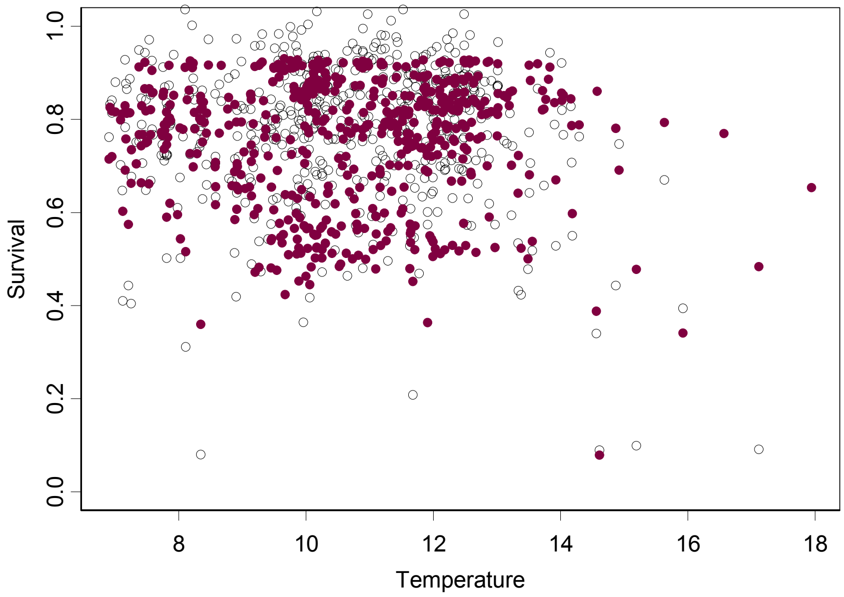

Figure 33. Modeled and observed Snake River steelhead survival vs. temperature (^{o}C) for migration from Snake River hatchery release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

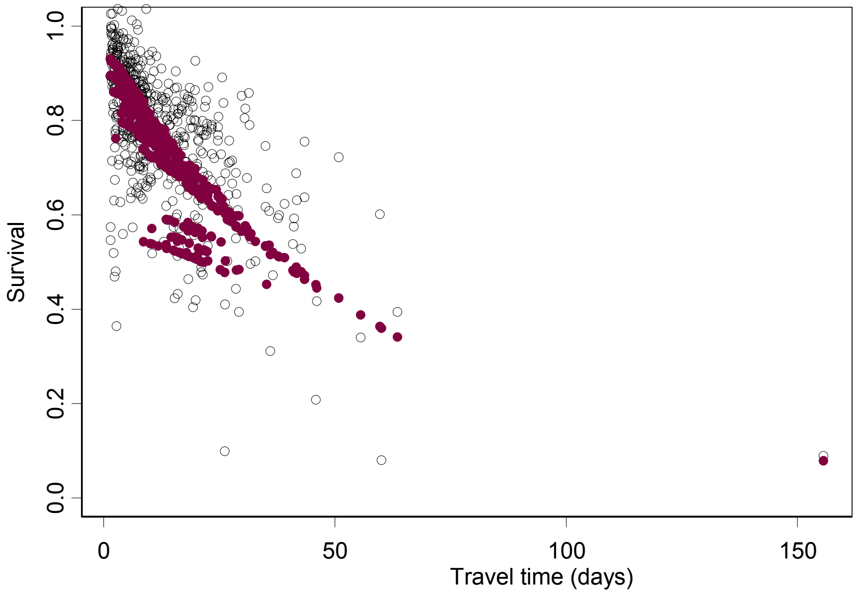

Figure 34. Modeled and observed Snake River steelhead survival vs. travel time for migration from Snake River hatchery release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

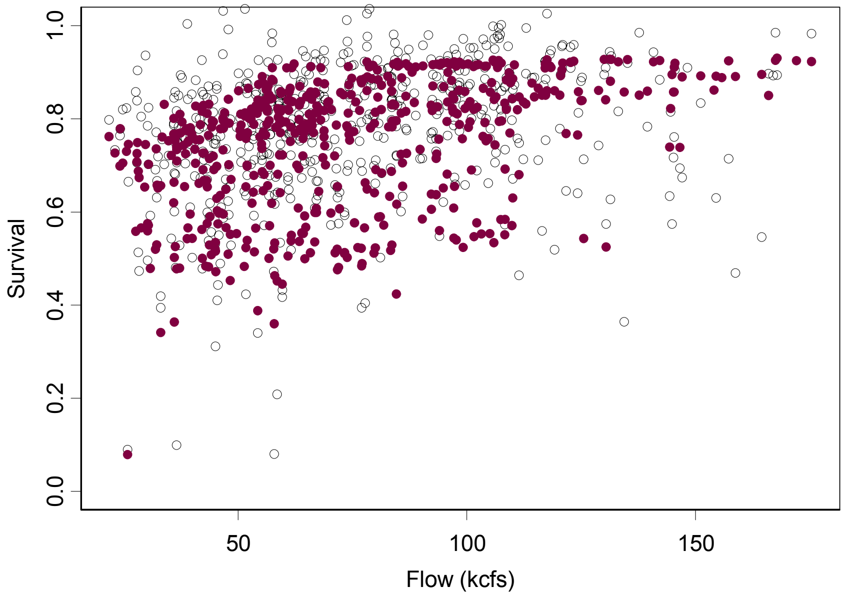

Figure 35. Modeled and observed Snake River steelhead survival vs. flow for migration from Snake River hatchery release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

Survival and water transit time

The model analysis developed here provides in theory and observation a creditable ecologically based explanation for the patterns of survival in chinook and steelhead juvenile migration. However, using essentially the same data other analyses have illustrated a relationship between smolt survival and a surrogate flow measure, the water travel time (SFTAFM 2002). The analyses used multiple correlations to claim statistical correspondence between water travel time (a flow surrogate), temperature and spill. The SFTAFM analysis and the analysis here both conclude temperature and spill are factors in the smolt survival. However, in terms of the impacts of flow, or its surrogate water travel time, the two analyses reach diametrically opposed conclusions. To reconcile these differences I have conducted an analysis similar to the SFTAFM analysis of survival vs. water travel time over the reach LGR to MCN. The results of the SFTAFM analysis and my analysis for spring chinook and steelhead are illustrated in Figure 36 through Figure 39. The analysis here yields similar results with a significant linear regression between survival and water travel time over the reach. The slopes, intercepts and r-squares are similar although the exact values depend on how the data are grouped. In any case, using data between 1998 and 2002 survival decreases with increasing water travel time.

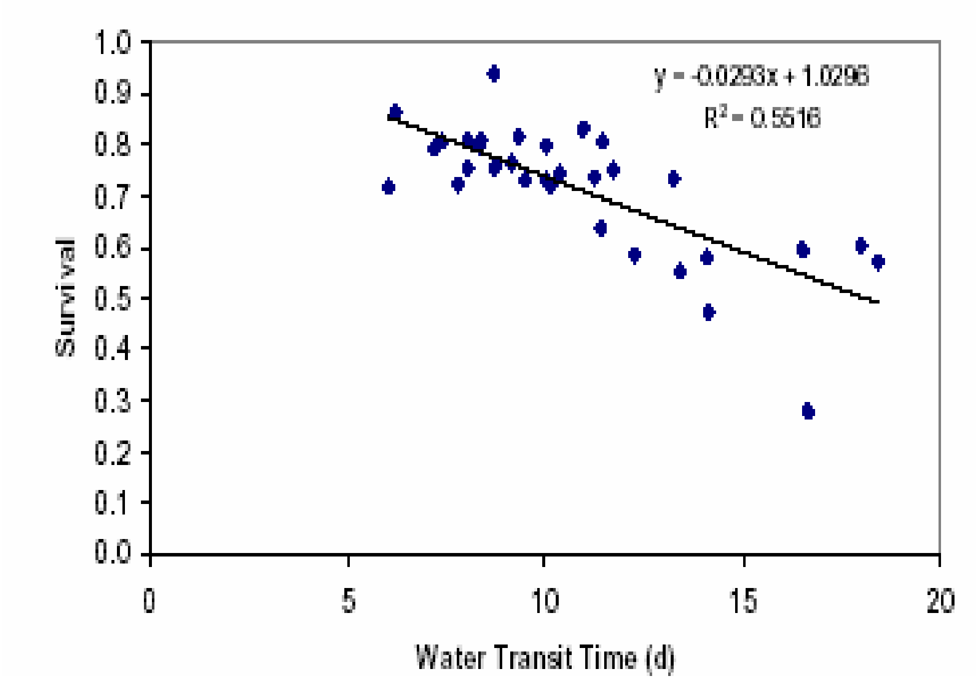

Figure 36. Hatchery spring chinook survival vs. water transit time from LGR to MCN 1998 to 2002 (SFTAFM 2003).

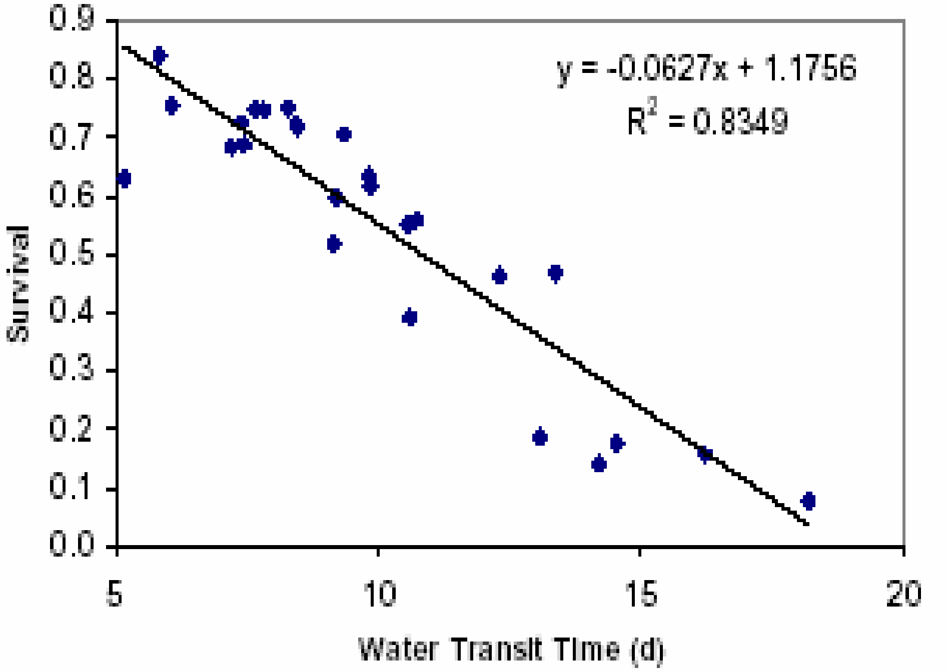

Figure 37. Hatchery steelhead survival vs. water transit time from LGR to MCN 1998 to 2002 (SFTAFM 2003).

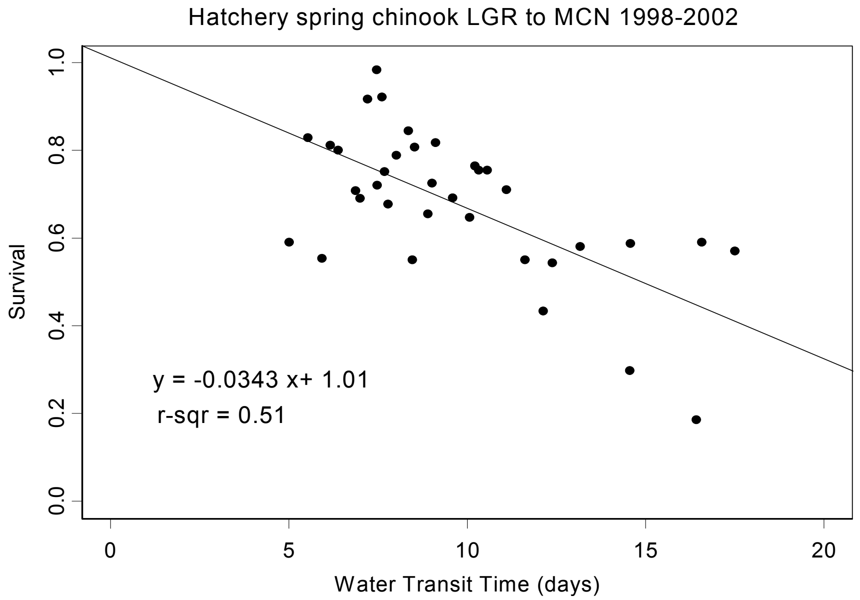

Figure 38. Hatchery spring chinook survival vs. water transit time from LGR to MCN 1998 to 2002 from the data in this report grouped by week of release.

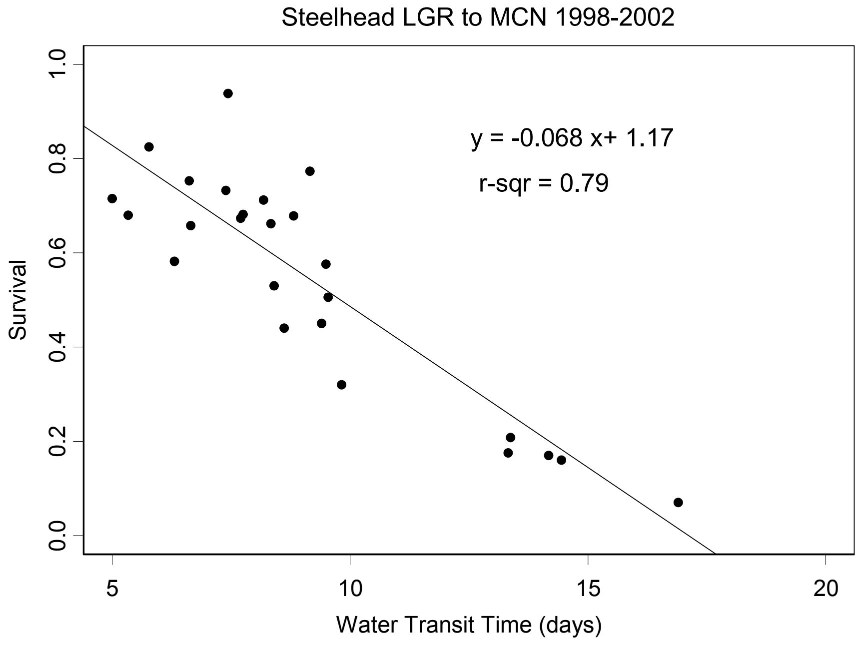

Figure 39. Hatchery steelhead survival vs. water transit time from LGR to MCN 1998 to 2002 from the data in this report grouped by week of release.

If, however, one were to assume that the correlation is a result of water travel time and the relationship is continuous, so that increasing travel time results in decreasing survival, then one would assume wrong. This is readily demonstrated in Figure 40, which illustrates that the year 2001 drives the negative correlation. Excluding the warm low flow year 2001 from the group results in the relationship disappearing. Thus, 2001 with its high temperature and correspondingly low flow and survivals drives the regression. However, as was demonstrated in the previous section, the high temperature in 2001, not flow, is sufficient to explain the survival pattern between years and within each year.

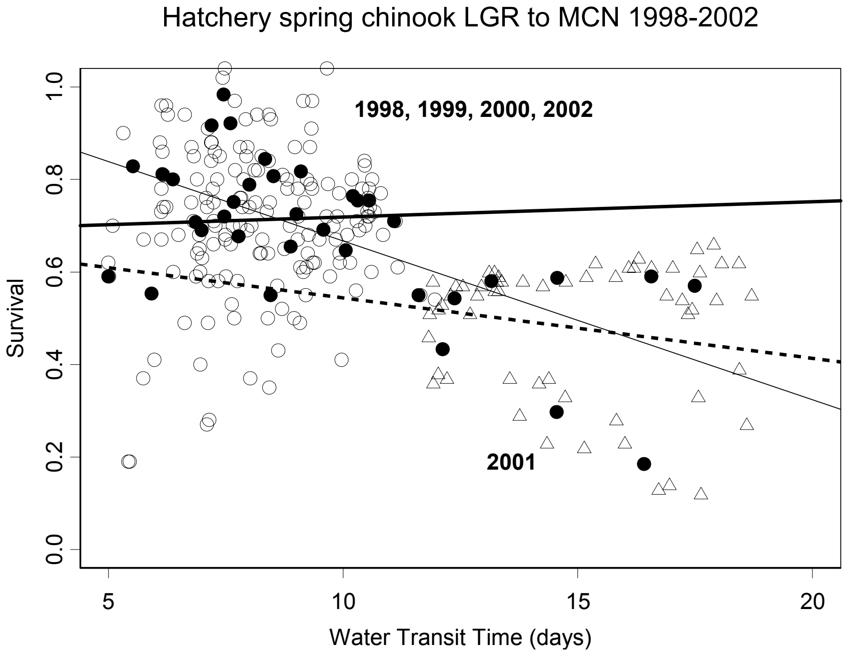

Figure 40. Hatchery spring chinook survival vs. water transit time from LGR to MCN 1998 to 2002 from the data in this report. Daily survivals vs. water transit time for the years 1998, 1999, 2000, and 2002 are designated by (○). For this data, the survival vs. water transit time has no significant slope. The daily data for 2001, designated by (Δ), has a small but insignificant negative relationship between survival and water transit time. Only the combined data grouped by weeks, designated (●), exhibits a negative relationship between survival and water transit.

Summary

The XT- model was developed as an ecologically based explanation of observations in which smolt survival was independent of fish travel time. This result seems at first perplexing because we expect survival to depend on the time the prey are exposed to the predators. The XT-model, which is based on molecular collision theory, provides a mechanism for this observation. In the model, if predators are relatively stationary and the prey migrate directly through the predator habitat then the prey experience a gauntlet of predators and mortality depends on the number of predators encountered, which is related to the migration distance. In the XT-model, survival can also depend on travel time and the balance of distance and time in determining survival depends on the average migration velocity of the prey relative to the random encounter velocity between predators and prey. Besides these two velocity scales, survival depends on the cross-sectional encounter area for predation events and the predator density. These processes are defined in the XT manuscript (Anderson, 2003) and will be submitted to American Naturalist (Anderson and Zabel, manuscript). In new work presented here, the model is extended by relating the encounter area to water clarity and predator density to temperature. The visual range of the predator describes the encounter area and the effective predator density depends on the predator activity, which for predatory fish is strongly determined by water temperature. The final model contains four model variables: temperature and turbidity exponents, the random encounter velocity and a predator length scale. Survival depends on prey migration distance and migration travel time and the temperature and turbidity. An analysis of survival in different species and runs of juvenile fish that migrate through the Snake/Columbia River system indicate that not all factors have equal importance.

In this manuscript, the factors affecting smolt survival were explored with the XT-model. Two regions were evaluated, the hydrosystem between Lower Granite Dam and McNary dam and the Snake River tributaries between upriver release sites and Lower Granite Dam. Two species were evaluated: chinook and steelhead. In the hydrosystem, suitable results were obtained by combining the spring and fall runs of chinook while in the tributaries the spring and fall runs were evaluated separately.

A number of patterns emerged from the analysis, which shows consistency with ecological theory and information on the life history of these fish. In the hydrosystem, survival was represented best through migration distance and temperature. Turbidity and travel time have insignificant impacts on survival of both chinook and steelhead. The temperature exponent, which best fits the data, was about $m = 3$ for both species. In theory, this coefficient should depend on the predator activity; independent laboratory feeding experiments (Vigg et al 1991) fit a similar exponent value. The model calibrated with the combined data over all years fit well the survivals of fish in both high and low flow years corresponding to years with low and high water temperatures. Note worthy also, the coefficients that fit the normal years also fit well the very low flow year 2001 for both steelhead and chinook.

The analysis of data from the tributaries suggests more varied processes effect these early stages of migration. Spring chinook survival only correlates with distance traveled. Neither travel time, temperature, nor turbidity exhibit significant correlations with survival. The data exhibit a considerable amount of scatter, which I attribute to the varied passage histories of the fish combined into a single analysis. The spring chinook, groups that migrated different distances were from individual hatcheries with different rearing histories and they essentially migrated through different river systems on their journey to Lower Granite Dam.

The steelhead survival data from the tributaries is similar to the spring chinook data in that they had different rearing histories and migrated through essentially different rivers. Steelhead survival, like that of the spring chinook, was independent of river temperature or turbidity, and was dependent on migration distance. However, unlike the spring chinook, the steelhead survival was correlated with migration travel time. The model captures this relationship with a large random encounter velocity, suggesting that the early migration behavior of the steelhead is significantly different from that of the spring chinook. Although steelhead survival depends on travel time as well as travel distance, no correlation between survival and flow was found. I attribute this to a commonly observed decoupling of migration velocity and water velocity during the early stages of migration in both salmon and steelhead (Zabel et al 2001, Zabel 2002).

Fall chinook survival in the tributaries exhibited the most interesting pattern. The model analysis suggests that all factors, temperature, turbidity migration distance, and migration time contribute to their survival.

XT-model implications to flow management

To use this analysis to address the impact of flow on smolt survival, first note that the model does not include flow. Any impacts of flow must act indirectly through impacts on the environment, specifically temperature and turbidity, or through water velocity that then affects fish velocity. An even more indirect effect could be through an impact of flow on the distributions of predators and prey. In particular, 1997 was a year with very high flows and very long travel times for fish down to Lower Granite Dam (Anderson 2003). This year was anomalous among all others; presumably, the flood altered the migration behavior of the prey and foraging behavior of the predators. Excluding this anomaly, which is fully natural and cannot be recreated or diminished with regulation, water management actions that alter flow should act in terms of temperature, turbidity and fish velocity. Thus, addressing how flow management affects fish requires first addressing how flow management affects temperature, turbidity, and velocity, and second, addressing how these variables affect smolt survival.

Consider first the physical question how flow management affects water temperature, turbidity and velocity. We know flow augmentation from the Snake River can increase the water temperature, if the augmentation is from the Hells Canyon complex (Anderson 2001), or it can decrease the temperature if augmentation is from the Dworshak Reservoir. Water withdrawals presumably decrease water temperature, but to a first order, the effect should only be significant in the small tributaries. In the mainstem, is difficult to see how water withdrawals affect the river temperature. Flow augmentation and water withdrawals have virtually no impacts on water velocity and fish velocity in the mainstem of the river system. In very small tributaries, these actions could affect water velocity. However, in the tributaries fish velocity is largely decoupled from water velocity.

Considering the biological question next, if flow management actions affect the physical processes how in turn do the physical processes affect the fish ecology and ultimately their survival? Here the XT-model provides a way to view the problem. In the mainstem, fish travel time has virtually no impact on their survival while temperature does affect fish survival. Considering the linked physical and biological processes, mainstem water management actions may have very little effect on survival. The actions have no meaningful impacts on velocity and fish travel time does not affect their survival. Although temperature is highly important to fish survival in the mainstem, management actions have no meaningful impacts on temperature. Therefore, in the mainstem there is no apparent link between flow and survival in theory or in the data.

In the tributaries spring chinook and steelhead survivals exhibit no correlations with temperature or turbidity. Even though we expect flow management actions may affect temperature the impacts on these species is insignificant. Flow management actions can have some small effect in the tributaries but the biological link to spring chinook appears missing because survival in this group is independent of travel time. With steelhead, although survival depends on travel time, travel time does not correlate with flow and again, there is no obvious link between the existing flow management and steelhead survival in the tributaries.

For fall chinook above Lower Granite Dam temperature, turbidity, travel time and travel distance all appear to affect their survival. In this region, flow management would have mixed impacts. Flow augmentation from the Hells Canyon system would tend to increase water temperature slightly (Anderson 2001) and therefore it would be detrimental to fish survival. Dworshak augmentation lowers the temperature and so this could improve survival of the fall chinook once they reached the confluence of the Snake and the Clearwater rivers.

Although it is possible to qualitatively link flow management actions to the physical river conditions and then to fish ecological conditions and survival, the actual impact of management actions, on top of the natural seasonal and year-to-year variations in flow and water properties, is minuscule. Thus, even though we are making some progress towards understanding the complexities of the system, my early conclusion on the impacts of flow management on smolt survival (Anderson 2002) remain unchanged. Flow augmentation and water withdrawals in the major river systems have no effect on smolt survival.

Finally, considering the strength of my conclusion we need to address how other analyses (SFTAFM) have demonstrated a statistically significant and consistent relationship between smolt survival and water transit time, which is a surrogate for flow. I suggest the relationship is spurious and is wholly dependent on the data from 2001, which was a year with low flow and high temperature. The conclusion from my analysis is that temperature, not flow, produced the correlation. Remove 2001 from analysis of survival with water transit time and the correlation disappears. In contrast, remove 2001 from the XT-analysis and the correlation with temperature and travel distance remains, and is equally significant.

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