February 7, 2003

Mr. Mark Walker
Director of Public Affairs
Northwest Power Planning Council
851 S.W. Sixth Avenue, Suite 1100 e-mail: comments@nwppc.org
Portland, Oregon 97204

RE: Comments on the Council's Draft Mainstem Amendments, Document 2002-16

Dear Mr. Walker:

Thank you for the opportunity to submit comments on the above referenced Draft Amendments (Draft). We appreciate the opportunity to provide these comments in support of the Council's Draft. Also, we appreciate the Council's hard work preparing the Draft in the face of conflicting information and the contentious issues that must be addressed.

These comments are submitted on behalf of the Committee of Nine and the Idaho Water Users Association (hereinafter "Idaho water users"). The Committee of Nine is the official advisory committee for Water District 1, the largest water district in the State of Idaho. Water District 1 is responsible for the distribution of water among appropriators within the water district from the natural flow of the Snake River and storage from U.S. Bureau of Reclamation reservoirs on the Snake River above Milner Dam. The Committee of Nine is also a designated rental pool committee that has facilitated the rental of stored water to the Bureau of Reclamation to provide water for flow augmentation (FA) pursuant to the 1995 and subsequent Biological Opinions. The Idaho Water Users Association was formed in 1938 and represents about 300 canal companies, irrigation districts, water districts, agri-business and professional organizations, municipal and public water suppliers, and others.

As evidenced by our past comments[1] to the Council and federal agencies, the Idaho water users' primary concern is the continued use of water from the Snake River above Brownlee (upper Snake) for FA in the name of recovery for ESA listed salmonids. We fully support the recommendation regarding FA at Lower Granite Dam and offer additional evidence below as to why the 2000 FCRPS Biological Opinion flow objectives should not be hard constraints. Discussions regarding the use of water from the Bureau of Reclamation's upper Snake River Basin projects for FA are ongoing as part of court

[1] The Idaho water users have submitted 17 separate sets of comments since October 1999 urging the use of FA from the upper Snake be discontinued or reduced, and certainly not expanded.

ordered mediation in the Snake River Basin Adjudication. We concur in the Council's recognition that any use of water from those reservoirs for FA must be pursuant to applicable state law including the state law provision that requires water for FA only be available from willing sellers.

Regardless of whether the issue of releasing water from the upper Snake for FA can be resolved in the ongoing mediation, we continue to support the recommendations of Giorgi, et al. 2002, "Mainstem Passage Strategies In the Columbia River System: Transportation, Spill, and Flow Augmentation," which call for a comprehensive evaluation of the flow management recommendations of the 2000 BiOp. Those recommendations include the last paragraph of Section 3.5 which states:

> *Given the community's sensitivity to this controversial management action, a holistic comprehensive updated evaluation seems prudent, and long overdue.*

Further, we support the conclusion at the end of Section 3.6 of the report which states:

> *To fully address concerns regarding anadromous fish and resident fish will require a significant effort. But without such an effort it is not clear how the region can determine if the status quo as prescribed in the FCRPS is an effective water management strategy for measurably improving salmon survival.*

As part of the recommended evaluations and until such analyses are completed, we urge the Council to consider the attachments included with this comment letter. The first attachment, "The Flow Survival Relationship and Flow Augmentation Policy In the Columbia River Basin," by Dr. James J. Anderson, September 2002, gives a brief history and evaluation of the existing flow augmentation practice in the Columbia River basin. Dr. Anderson's conclusion is the growing body of science and data does not support continuation of the 2000 BiOp flow measures.

The second attachment titled "A Collision Theory Based Predator-Prey Model and Application to Juvenile Salmonids in the Snake River Basin," by Dr. James J. Anderson, which will be submitted to the American Naturalists with his co-author Richard W. Zabel in 2003, offers an alternative model to analyze passage of listed salmonids through the mainstem Snake River. The model, known as the XT model, is based upon well established molecular collision theory to simulate the interaction of prey, listed salmonids, and predators through the mainstem Snake River.

The third attachment titled "An Analysis of Smolt Survival with Implications to Flow Management," by Dr. James J. Anderson, 2003, applies the XT model to the existing survival data for the mainstem Snake and Columbia Rivers. The PIT tag data collected in recent years for anadromous fish passing through the mainstem Snake and Columbia Rivers makes possible a clearer understanding of the mechanics of fish passage through the river environment. The calibrated XT model reproduces the observed survival (PIT tag) data very well and further contradicts any scientific support for a flow-survival relationship through the mainstem let alone a FA-survival relationship or a flow objective-survival relationship.

In addition to the reasons described in Dr. Anderson's work above, the Idaho water users have long believed the Lower Granite flow objectives are not appropriate from a hydrologic standpoint and do not represent river conditions that ever occurred in the past century. Figure 1, below, shows the mean annual discharge of the Snake River at Lewiston for the period 1911 – 2002. The trend line shows there has not been a significant change, either increase or decrease, in mean annual discharge for the period but makes apparent the large yearly fluctuations that do occur. Figure 1 also shows 1997 had the highest mean annual discharge for the period of record and 1995 is approximately a median year for the period.

Figure 1.
Mean Annual Discharge - Lower Granite Inflow

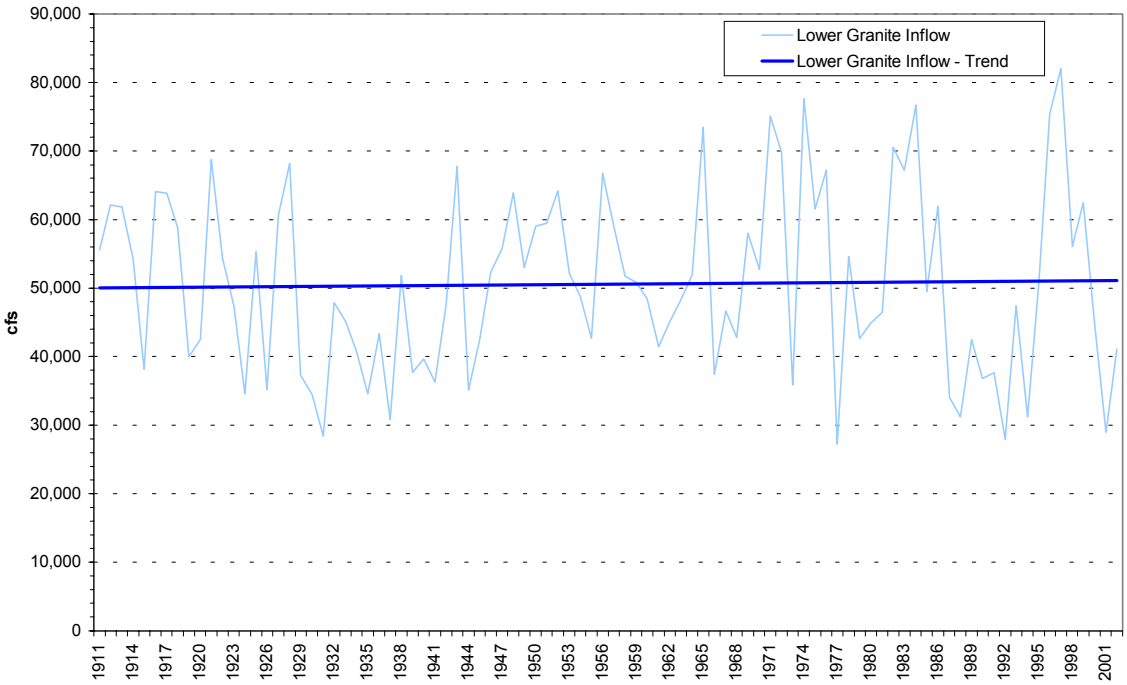

Figure 2 is the annual hydrograph for the Snake River at Lewiston for 1997 and 1995 relative to the 2000 BiOp flow objectives[2]. The figure shows the flow objectives, even with FA, were not fully achieved in 1997, the highest runoff year of record. The figure also shows the flow objectives were achieved less than half the time in the median year 1995 with FA. These facts support and strengthen the Council's position that the Lower Granite flow objectives cannot be hard constraints and are not appropriate goals for river management since they do not reflect conditions that can be achieved in the river.

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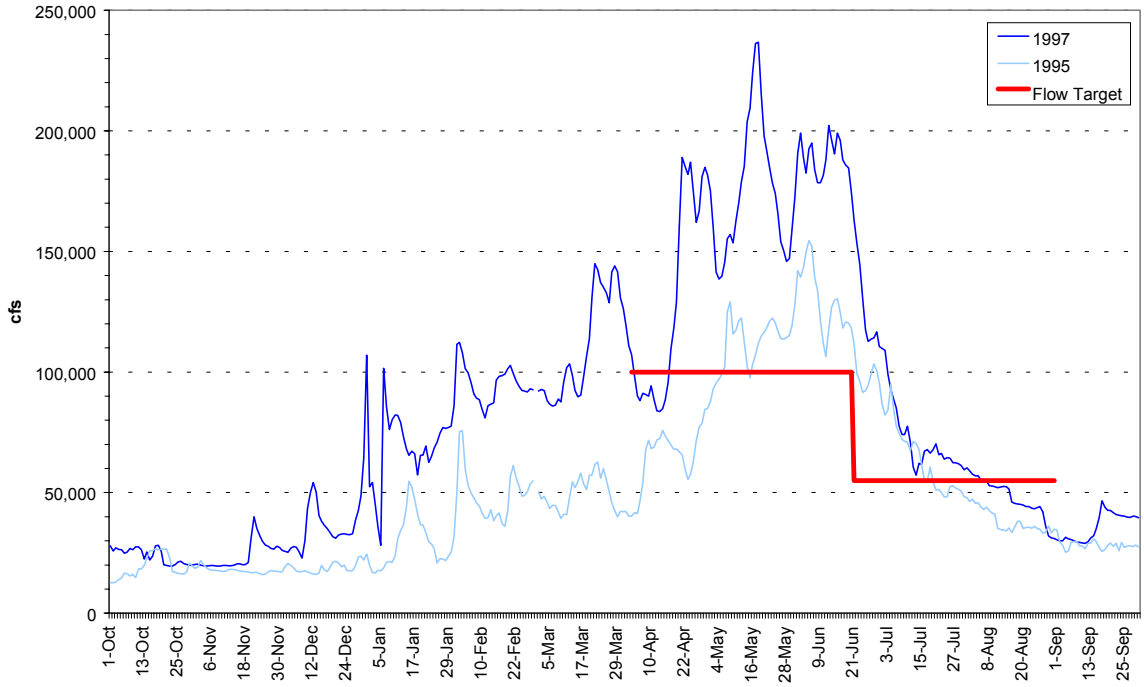
[2] The 2000 BiOp specified Lower Granite Flow Objectives in the spring of 85,000 – 100,000 cfs from April 3 through May 20 and in the summer of 50,000 – 55,000 cfs from May 21 through August 31. The spring flow objective was 100,000 cfs for both 1995 and 1997 and the summer flow objective was 52,300 cfs for 1995 and 55,000 for 1997. Figure 2 shows 100,000 and 55,000 cfs, 52,300 cfs would be approximately half way between the summer flow objective shown and the 50,000 cfs grid line.

Figure 2.
Lower Granite Inflow



We want to stress the upper Snake storage projects are in place for specific purposes and are not a part of the FCRPS. While we generally agree with the Council's recommendations for study and management of the FCRPS storage projects, those same recommendations are not appropriate if they were to be applied to the upper Snake projects. The upper Snake projects should be operated according to the project authorizations, primarily for the benefit of contract water storage space holders, and not as part of the FCRPS. If the SRBA mediation leads to the release of water from the upper Snake in an attempt to benefit listed anadromous species, the releases should be considered off-site mitigation since the upper Snake projects are not part of the FCRPS and did not cause the decline of the listed species. Taking water from the upper Snake will not recover the listed species but it can cause damage to resident fish and wildlife and creates an unnecessary economic burden on portions of the State of Idaho.

The issue of reintroduction of anadromous fish upstream from the Hells Canyon project is being addressed in the FERC relicensing for the project. We agree with the Council's recommendation that reintroduction questions be resolved in the FERC relicensing process. For the record, the Idaho water users are on record opposing reintroduction of anadromous fish upstream from the Hells Canyon project.

We support the Council's position regarding the effect of adoption of the Draft on the Council's 1994-95 program. Specifically, adoption of the Draft should supersede all provisions, objectives and measures of the 1994-95 Columbia River Basin Fish and Wildlife Program including all of Sections 5 and 6. The Council has appropriately taken

into consideration new data and science reflecting present conditions as the basis for the Draft. When the Draft is adopted, there should be no uncertainty that the Council intends to move ahead with a new Fish and Wildlife Program based on the most recent data and science available. Making a clear departure from the 1994-95 program will aid the region to move ahead with implementation of the new Fish and Wildlife Program.

As stated above, we support the Council's Draft and the Council's preferred alternative selected in the Draft. We believe that the preferred alternative for the Fish and Wildlife Program is based on good science and good data that reflect reservoir operations and stream conditions that we believe will aid recovery of the listed species while protecting non-listed species, both resident and anadromous, and the economy of the region. The Council's rejection of alternative G in the Draft is essential for the economic health of the region. Alternative G proposes measures that are not supported by science, that will not lead to recovery of the listed species, and that will add $42 million to the region's annual power cost. Additionally, alternative G would reduce agricultural income by $80 to $369 million per year in Idaho as estimated by the Bureau of Reclamation. Our analysis shows the loss to Idaho agriculture would be higher. Alternative G should not be given further consideration as a viable part of the Council's Fish and Wildlife program.

We appreciate this opportunity to provide comments on the Council's Draft Mainstem Amendments and commend the Council for the careful consideration and hard work they put into the Draft.

Respectfully submitted by,

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The Flow Survival Relationship and Flow Augmentation Policy in the Columbia River Basin

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September, 2002

Corrected 9/9/2002

Flow augmentation and flow targets have been central programs in Columbia River salmon management for more than twenty years. Over this time, water requests have increased from 3.75 MAF in 1983 when the Water Budget was established (NPPC 1983) to between 13 and 16 MAF in the 1995 and 2000 NMFS Biological Opinions (NMFS 1995a; NMFS 2000a). Over the same period, the body of science on the effects of flow grew from a single graph between smolt survival and Snake River flow, to a body of information involving the tagging of a million smolts with survivals measured over the entire salmon life cycle. Whereas the growing body of scientific evidence indicates that variations in flow have no measurable effect on survival of juvenile salmon and steelhead

through the mainstem of the Columbia and Snake, the fish managers continue with their policy of augmenting these flows and have effectively halted further withdrawals of water from the mainstem of the system. In this paper I explore the history of the flow survival research and how political objectives produced a growing disconnect between the research and the water policy.

The development of flow policy

The flow augmentation policy established two decades ago is based on the initial research suggesting small changes in flow are correlated with large changes in fish survival. However, the policy is based on two assumptions 1) a flow survival relationship actually exists and 2) the effect natural flow variations have on survival can be achieved with flow augmentation.

Even prior to the completion of the hydrosystem National Marine Fisheries Service researchers (NMFS) documented the detrimental effect of dams on the survival and travel time of fish during their migration to the ocean. Prior to the construction of the Snake River dams (1964-1974), smolt traveled from the Snake River to the ocean in a matter of days and with the construction of the dams (1974-1994), the travel time extended to several weeks (Figure 1). Concomitant with the increasing travel time the percent of adults returning, designated the smolt-to-adult ratio (SAR) declined. While it was clear that fish suffered mortality as they passed the dams, there was also a concern that the extended travel time contributed to the fish mortality. The hypothesis was that extended travel times increased the exposure of fish to predators and disease and delayed their entrance into saltwater, resulting in additional stress and mortality both in the river migration and in the estuary. Researchers studied survival of smolts from the Snake River to John Day Dam over seven years. Based on two low survivals in years with very low flows they hypothesized that more flow produced higher smolt survival (Figure 2). The hypothesis became known as the Sims and Ossiander flow survival relationship after the NMFS scientists that published the finding in an annual research report (Sims and Ossiander 1981).

At the same time as with the construction of the hydrosystem, the Columbia and Snake River salmon stocks declined and so fish managers sought a number of partial solutions

to restore the runs. The two main actions were limiting harvest and increasing the production of hatchery fish to compensate for habitat lost by the dams. In addition, fisheries managers sought to increase survival by bypassing smolts around the turbines and by speeding their seaward migration by flushing additional water through the river during the spring migration. The initial flow augmentation occurred in 1983, and was base on two premises. One was intuitive. Because smolts migrated during the spring flushet and the dams diminished the spring flows, augmentation of the spring flows with water from the storage reservoirs would partially mimic the natural conditions and therefore increase smolt survival. The second premise was quantitative. The Sims and Ossiander flow survival hypothesis suggested great benefits from modest increases in flow. For example, fish managers predicted spring chinook survival would increase 180% with a 47 kcfs increase in flow at Ice Harbor Dam (CBFWA 1990). However, applying the Sims and Ossiander curve to predict the benefits of flow augmentation involved a very important, but unstated, assumption. The Sims and Ossiander curve was derived by plotting yearly averaged flow against yearly average survival and thus represented a relationship between years. Flows between years depend on the amount of rainfall, snow, and the temperature patterns, which together control environmental conditions prior to and during the smolt migration. Thus, a yearly average flow survival relationship involves many factors other than just the flow that the fish experience while migrating through the river. Flow augmentation, however, is produced by shaping the available flow within the season. Thus, by applying the Sims and Ossiander curve to flow augmentation fish managers assumed that the benefits of a wet year could be achieved in a dry year by simply reshaping the timing of the spring runoff.

Two decades ago when the Water Budget began, neither the flow survival hypothesis nor the hypothesis on the equivalence of natural and augmented flows were challenged and in fact they was simply not discussed. However, these assumptions were central to the Water Budget in 1983. Thus, the fish water policies today have a direct lineage to the curve Sims and Ossiander drew through seven data points representing observations of (1973-1979) yearly averaged flows at Ice Harbor Dam against the per project survival of spring chinook and steelhead smolts from the Snake River to John Day Dam.

Testing the hypothesis that survival increases as flow increases

Over the past two decades, flow was hypothesized to affect survival via the effect of flow on travel time, altering the exposure of fish to predators and deleterious river conditions. While studies establish that flow was related to travel time, the Sims and Ossiander flow survival hypothesis could not be reproduced. A weaker relationship between flow measures and SARs was identified but the underlying factors could not clearly be identified which prompted a revision of the flow survival mechanism to include other factors such as estuary arrival timing. Even though the research has not supported the hypothesis, fish managers have not abandoned the flow policy based on the hypothesis but instead increased flows even more based on the hypothesis.

Although the Sims and Ossiander flow survival hypothesis is critical to fish water policy, it has never been precisely formulated, and the hypothesized underlying mechanism has changed over time in response to findings of the flow survival research. In the initial mechanism, it was hypothesized that flow affected survival via its effect on fish travel time: Increased flow decreased fish travel time, which increased fish survival. Petrosky (1992) demonstrated an inverse correlation between travel time of Snake River water and the survival of smolts to adult (SAR) (Figure 1). A paper by Berggren and Filardo (1993) provided support for the travel time mechanism by showing flow and smolt travel time were significantly related for Snake River spring chinook. Hilborn (1993) compared SARs of spring chinook from the Upper and Lower Columbia and concluded the SAR difference between the two reaches was greater for years with lower flows. Cada et al. (1994) reviewed a range of studies and suggested other factors were also of importance, especially temperature. With these reports, NMFS established a flow augmentation policy in the 1995 Biological Opinion (NMFS 1995a, b). The dominant justification was in terms of the flow-travel time link. NMFS used travel time as one of the main performance measures in setting the spring and summer flow targets the hydrosystem required to insure safe passage of smolts. The flow target justification also involved temperature: fish arriving at projects later with higher temperatures would encounter more active predators and could have lower bypass efficiency causing more fish to pass through turbines. Thus, the water policy, up through the 1995 Biological Opinion, was based on a handful of studies that appeared to support the Sims and Ossiander assumption

that increases in flow increase salmon survival. There was no test and little discussion of the second assumption that the benefit assumed from natural year-to-year flow variations could be achieved by reshaping flows within a year.

However, with the development of the PIT-tag marking system, which allowed greater precision in estimating smolt survival, scientists were able to fully test the first hypothesis and partially test the second hypothesis. The first test of the Sims and Ossiander flow survival hypothesis was obtained in Little Goose Reservoir in 1992. It was a low flow year similar to 1973 and NMFS researchers expected survival to be low, but surprisingly, the PIT-tag measured survival was higher than the highest survival obtained in the highest flow year of the Sims and Ossiander study. Results from 1994 also showed very high survival. It is noteworthy that in developing the flow targets for the 1995 Biological Opinion, NMFS rejected the 1993 and 1994 PIT tag studies (NMFS 1995b). However, with each additional year of data, the rejection of the flow-survival hypothesis became stronger: It is now clear that survival of spring chinook and steelhead through the hydrosystem is not related to variations in flow (NMFS 2000b; Bickford and Skalski 2000, Muir et al. 2001).

Researchers have reviewed the early studies and found flaws. The strong flow survival relationship in the Sims and Ossiander data (Figure 2) depended entirely on low survivals in the two drought years, 1973 and 1977. A closer look at the historical records revealed these low survivals were likely caused by poor dam passage conditions, not the low flows. Because the dam intakes were not regularly cleaned, larger numbers of tree, branches and other trash, accumulated at the face of the upper most dam on the Snake River (Williams and Matthews 1995). A review of the Petrosky's (1992) travel time and SAR relationship also revealed flaws with the analysis. NMFS used data representative of the current fish passage environment and found a weaker relationship between smolt to adult ratio (SAR) and water travel time (Figure 2) (NMFS 2000b). For the first time NMFS articulated the previously unquestioned second hypothesis stating, "Correlation does not necessarily imply causation (Sokal and Rohlf 1981), and higher SARs associated with higher flows does not necessarily indicate the SARs can be increased by adding more flow to the river" (NMFS 2000b, 53). Skalski, *et al.* (1996) revaluated the Hilborn *et al.* study (1993) and found that the relationship between SARs and flow

depended wholly on the choice of reference sites. Finally, Giorgi *et al.* (1997) found flow and travel time were not correlated for mid-Columbia fish. Thus, the flow travel time relationship Berggren and Filardo (1993) found for Snake River fish could not be universally applied.

Not withstanding the plethora of information seriously challenging the data and the theory on which the 1995 Biological Opinion was based, NMFS sustained its policy by concluding "that although a direct flow survival relationship cannot be established by data, it does not preclude benefits of flow augmentation because increased flows may improve survival outside the hydrosystem as a result of earlier arrival to the estuary, improved estuary conditions and reduced delayed mortality (NMFS 2000b, 58)." For the 2000 Biological Opinion NMFS continued to call for flow targets: "These results support management actions to provide flows of at least 85 kcfs in the Snake River and 135 kcfs in the upper (mid-) Columbia River during spring and 200 kcfs in the lower Columbia River during the summer (NMFS 2000b, 57)." Furthermore, NMFS implemented the "no net withdrawal" policy to preclude additional withdrawals of water from Columbia and Snake River Basins.

Newer research shows no flow survival relationship

The newest studies firmly rejected the flow-survival hypothesis. For yearly averaged data, which tests for a relationship between years, both in-river and SAR measures of survival were either independent of flow or exhibited statistically weak increases with flow. However, when comparing weekly or daily averaged data within each year, which tests for a flow survival trend within a season, no relationships were evident whatsoever.

Research published after the 2000 Biological Opinion strengthens the conclusion that flow is not related to survival. NMFS's scientists (Smith *et al.* 2002) wrote, "Correlations between river discharge and survival between Lower Granite Dam and McNary Dam and between travel time and survival were neither strong (within or between years) nor consistent from year to year." However, the paper took particular care to offer alterative theories under which the agency's policy might still make sense: "Thus, survival benefits to the stocks from increased flow in this stretch of the river were at best minimal; any measurable benefits occurred downstream from the Snake River.

(Smith et al 2002)". Going further, the publication speculated that flow augmentation during smolt migration might provide survival benefits in other portions of the salmonid life cycle and in free-flowing sections of the river both upstream and downstream from the hydrosystem. They suggested flow augmentation may improve the arrival timing of fish to the estuary citing a paper by Zabel and Williams (2002) that found the date of fish arrival to Lower Granite Dam in 1995 correlated with rate of return of adults. However, the example is not convincing. Zabel and Williams (2002) also found that arrival date only correlated with survival for in-river passing smolts in one year. For smolts transported though the river the opposite trend existed, the later arriving fish survived better and in 1996, no significant difference was found between release date and returning adults for either transport or in-river groups.

The question remains, then, does flow augmentation directed at fish migrating through the hydrosystem improve survival of fish in the tributaries above hydrosystem, in the estuary, or in the Columbia River plume below the hydrosystem? It is noteworthy that to the present time little research has been conducted to test the hypothesis that flow affects fish outside the hydrosystem (Giorgio *et al.* 2002). However, data does exist to address this issue. First, consider the evidence for a flow-survival relationship above the hydrosystem. Six years of NMFS studies (Muir *et al.* 2001) demonstrated that hatchery spring chinook survival from Snake River tributaries to Lower Granite Dam was significantly related to distance traveled, but not travel time. Since fish survival was not related to fish velocity, the data contradicts the flow/travel time survival hypothesis. Moreover, plotting over ten years spring chinook survival traveling the 116 km distance between Dworshak Fish Hatchery on the Clearwater River to Lower Granite Dam clarifies the picture (Figure 4). The flow survival relationship was flat over the very large flow range of 20 to 140 kcfs. Snake River fall chinook is the only stock exhibiting a correlation between flow and survival to Lower Granite Dam. However, the studies also demonstrated that survival was strongly correlated with release date, temperature, and turbidity (Anderson *et al.* 2000; Dreher *et al.* 2000; NMFS 2000b). These analyses all conclude that with the existing data, flow cannot be the identified as the operative variable affecting survival. Furthermore, travel time is not correlated with flow or survival in these data, so if flow were the operative variable it does not act through the

previously assumed mechanism involving exposure time. If flow affects survival, it would most likely work indirectly through the effect of temperature on smolts and their predators and through the effect of turbidity on the water clarity of the habitat. However, flow augmentation from the Hells Canyon Reservoir complex warms the Snake River, which would presumably increase predator activity and therefore decrease smolt survival (Anderson 2000b). The NMFS (2000b) report also noted that the relationship of flow and survival was variable and less pronounced within the hydrosystem between Lower Granite and Lower Monumental dams.

The information available to address the impact of flow augmentation on salmon survival below the hydrosystem is more problematic. For this assessment, several studies have compared the SARs or the log of the ratio of the recruits to spawners (ln(R/S)) with flow measures. However, if such correlations exist flow is not necessarily the causative factor. Changes in the hydrosystem over the years of observation and the natural variability in the ocean conditions that may correlate with the wet and dry years, and therefore, make it impossible to establish a clear cause and effect relationship between the natural year-to-year variations in flow and these indicators of survival (NMFS 2000b). Confining the analysis to years representative of the current hydrosystem, several studies show a relationship between SAR or ln(R/S) and a measure of flow during the migratory season. However, as noted a number of factors preclude associating the relationship with in river flows. NMFS (2000b) found over the years 1974-1994 a weak statistical relationship between water travel time and SAR for spring chinook but not for steelhead. Snake River fall chinook survival, expressed as the residuals of the spawner recruit curve, was uncorrelated with the flow during smolt migration (Anderson Hinrichsen and Van Holmes 2000), while for Marsh Creek spring chinook a relationship was found (Petrosky 1991). With selected data, yearly averaged relationships between flow and adult survival measures may or may not be found, but since about 90% of the Snake River smolts were transported, their exposure to the river environment was very limited. In contrast, Mid-Columbia stocks are not transported and they have flow-survival correlations. However, in the years of these studies the low flows correspond to warm ocean conditions, which produce poor salmon survival in the ocean (Mantua and Hare 1997, Anderson 2000). Therefore, survivals that correlate with high flows also correlate

with years of better ocean survival. NMFS sums up the SAR flow information up through 2000 as follows, "While it is not possible to establish a clear cause and effect relationship with these [SAR and ln(R/S)] data, it is not possible to rule one out" (NMFS 2000b p 54).

However, the real question is not whether SAR is related to the natural year-to-year variations in flow, but whether SAR is related to flow augmentation. Germane to this question is the recent data on in-season flow and SAR, which was not available when NMFS prepared the white paper (NMFS 2000b). With nearly 700,000 run of the river PIT tagged salmon and steelhead smolts and 5000 adult returns it is now possible to explore wheter an in-season flow SAR relationship exists for Snake River fish. Figure 5 shows the results for in-river passing wild spring chinook over the years 1995 to 2000. The data represent averages of groups of fish that passed Lower Granite Dam weekly. Regression lines of weekly averaged SAR vs. weekly averaged flow for each year reveal no flow survival pattern within a year or between years for Lower Granite Dam flows ranging between 50 and 200 kcfs.

Models and the flow augmentation hypothesis

Since the flow-survival studies conclusively demonstrate that the effect of flow augmentation on fish survival above, below, or within the hydrosystem is so small, if it exists at all, as to be unmeasurable, models must be used to assess the incremental and cumulative impact of flow augmentation. Since models are simplified, but quantitative, representations of our understanding, as the data improves, the models are updated and revised. The first models developed by NMFS twenty years ago reflected the extremely limited data available and predicted a strong flow-survival relationship. The models now used by NMFS and the Region, which are based on an additional decade of high quality data, contain no flow-survival relationship whatsoever. Analysis also indicate even moderate water withdrawals should have virtually no impact on fish survival.

It is important to realize that the flow augmentation volumes released from upstream reservoirs are extremely small compared to the natural variations in flow, and the irrigation withdrawals at issue in this action are smaller still. Consequentially, since the relationship of survival and flow is inconclusive over the scale of year-to-year variations

and flow and survival are uncorrelated over the seasonal scale, it virtually impossible to measure the impacts of flow augmentation on fish survival. Therefore, with present technology the second assumption that varying flow through augmentation produces the same effect as natural variations in flow is untestable. Thus, to extrapolate information derived from natural variations to flow augmentation we must use models. NMFS developed the first model of flow augmentation, which was no more than a fit of a two-parameter equation through seven data points (Figure 2) (Sims and Ossiander 1982). The equation is empirical, it has no basis in fish ecology, but fish managers readily accepted it as a valid description of the impacts of flow on smolt survival through the hydrosystem.

In the 1990s, two juvenile passage models, FLUSH and CRiSP, were developed or revised for use in the PATH process, a regional workgroup changed with evaluating the impacts of dam removal on the recovery of Snake River salmon (Marmorek 1998). The FLUSH model assumed that the fish mortality rate, the percent of the remaining population that dies each day, increases the longer fish are in the hydrosystem. The CRiSP model assumed mortality rate is constant over the migration. The FLUSH model, like the early Sims and Ossiander empirical model, produces a strong flow-survival relationship while the CRiSP model has a relatively weak flow-survival relationship. Because at the time of PATH there were no measurements of fish through the entire extent of hydrosystem, scientists calibrated the two models with the available data, which extended halfway through the hydrosystem. Due to the nature of the models, they produced essentially the same survivals to the midway point, but because the mortality rate in the FLUSH model strongly increases with fish travel time the predicted survival through the entire hydrosystem was less than half the CRiSP model prediction (~ 20% survival for FLUSH and ~40% survival for CRiSP). A panel charged with reviewing the two models believed that smolt mortality should increase strongly with travel time through the hydrosystem and weighted the FLUSH model over the CRiSP model.

After the PATH review, survival estimates over the entire hydrosystem were finally available to test the two models. NMFS estimated juvenile spring chinook survival from the tailrace of Lower Granite Dam to the tailrace of Bonneville Dam was 48% for the 1997 migration. The two model teams then provided their prediction. CRiSP model

developers estimated survival was 59% and the FLUSH model developers estimate survival was 24%. In the next two years, NMFS provided additional hydrosystem survivals, which the CRiSP model team compared to their model predictions. For the 1998 smolt passage, the NMFS estimate was 63% and the CRiSP prediction was 49%. For 1999, the NMFS estimate was 56% and the CRiSP prediction was 54% (CBR 2000). The FLUSH modelers did not provide model either year, but by reverse engineering the FLUSH model (the actual model was never released to the scientific community), the estimated survivals for the two years would be below 15%. The results are clear, the FLUSH model and PATH scientific review panel's weightings are not supported by the survival studies.

NMFS was well aware of the failure of the FLUSH model and the difficulties of the PATH process so they develop an alternative model, SIMPAS, which is based on PIT tag survival studies between 1992 and 1999 (NMFS 2000c). Most significant, the SIMPAS model describes survival through the hydrosystem on a per kilometer basis. That is, the new NMFS model contains no flow survival relationship whatsoever. Furthermore, NMFS used SIMPAS in developing the 2000 Biological Opinion.

Thus, over two decades of modeling the impacts of the hydrosystem on juvenile salmon migration NMFS has progressed from a model with a very strong flow-survival relationship to a model with no flow-survival relationship. This surprising result may seem at first counterintuitive. NMFS in 1980, and the PATH review panel in 1997, both believed that fish mortality through the hydrosystem depends on how long it takes smolts to migrate through the system. In addition, both groups of researchers believed that the rate of mortality strongly increased over time so that the majority of the fish must die at the bottom of the hydrosystem. How then can survival be independent of the migration time? Anderson and Zabel (in review) developed a mathematically rigorous and intuitive explanation. Simply put, they showed that smolt survival is independent of travel time if the predators are essentially stationary. In this case, the smolts must pass a gantlet of predators and the total mortality does not depend on how fast the smolts migrate but on how many predators they encounter while passing through the hydrosystem gauntlet. (It should be noted that predator densities are in fact higher below the dams than within the hydrosystem; migrating salmon experience a gauntlet nearly everywhere they go.)

Against the gauntlet description, flow proponents have suggested that fish mortality increases with passage time as a result of cumulative stress experienced by the migrating fish (Budy et al. 2002). Although questions on the significance of stress are yet to be resolved we can summarily disregard the contribution of flow augmentation and water withdrawals to the fish stress levels because these actions only change the total travel time of the fish by minutes over a total migration of weeks.

Over the last few years, the CRiSP model has been used to estimate the impacts of flow augmentation and water withdrawals on smolt survival and in each case, the impacts are insignificant (Anderson 1999). For example, a 147 cfs withdrawal from the mid-Columbia was estimated to reduce adult returns by less than 9 fish out of a population of a half million and the travel time would be increased by minutes.

The new data and model trim even these estimates. From our recent studies, smolt mortality depends more on distance traveled than travel time, and the predicted impacts of flow augmentation in the updated model will be about 75% less than the impacts predicted in the previous model. Thus, where the CRiSP 1.6 model predicted a 9 fish loss the updated model, CRiSP 1.7, will predict about a two fish loss. However, even this miniscule modeled loss is higher than what is expected to happen in the real world. In previous evaluations of the impact of flow augmentation, we assumed that water withdrawn for municipal or agricultural uses is lost to the system. In fact, the majority of water pumped from the mainstem of the Columbia River system returns to the system, either as treated water or as ground water recharge. Thus, the impact need to be lowered in proportion to water actually lost relative to the amount withdrawn. In the above example, the predicted impact of a 147 cfs withdrawal is expected to be less than one adult salmon. Alternatively, using the new NMFS SIMPAS model the impact is zero fish lost.

Is the addition or loss of one or even a hundred adult salmon out of a population of a half million significant to the salmon populations? On an intuitive level, the answer is clearly no. Using models, NMFS recently concluded that recovery of Snake River salmon was not dependent on further improvements in hydrosystem survival (Kareiva *et al*. 2000). Moreover, NMFS has also concluded that even large reductions in adult returns are not

significant to recovery, as evidenced by the fact NMFS allows the in-river harvest of thousands of salmon in the mainstem of the Columbia River that would otherwise reach their final destination in a few weeks.

The disconnect between policy and science

While the cumulative body of scientific information all points to flow not affecting survival in any meaningful context, the policy of reducing water withdrawals and augmenting river flow has continued to expand. Furthermore, fish and water managers have consistently acted to discredit or ignore the information against their policies

The hypothesis that higher flow will improve fish survival was first proposed in 1981which led to the establishment of the Water Budget in 1983. Over the next two decades, only five additional studies and reports provided any indirect support for the hypothesis while more than twenty studies have directly refuted the hypothesis (Table 1). The evidence is now overwhelming to reject the hypothesis and the contention that flow augmentation and water withdrawals in the mainstem of the river system have any impact on salmon. However, over this same period the fish and water managers have increased the flow augmentation and implemented stringent regulations stopping water withdrawals (Table 1). Furthermore, as the research has serially addressed and rejected the hypothesis on which the water policy was based the managers have reformulated the hypothesis into more nebulous forms.

In 1983, the justification for the water budget was to speed fish down the river to increase survival. When this was shown to be false, the justification was switched to an impact on adult returns (SARs). When it became clear that the benefits of water policy could not be demonstrated in terms of adults returns the managers shifted justification saying that the research could not rule out benefits {"While it is not possible to establish a clear cause and effect relationship with these [SAR and ln(R/S)] data, it is not possible to rule one out" (NMFS 2000b p 54)}. When models demonstrated that the benefits of water policy were insignificant managers rejected the model (in the case of CRiSP) [Barwin transcript] or simply ignored the model (in the case of SIMPAS). When models predicted miniscule impacts managers challenged the conclusions applying a *reduction ad absurdum* proof, noting that a miniscule impact is significant if the entire river is withdrawn. In the face of

the accumulating evidence *against* the benefits of flow, managers continue to rely on non-deductive logic, statements of belief, and qualitative extrapolations: "Additional water withdrawals have the probable affect of exacerbating the situation thus delayed or prevent recovery of listed fish" [Barwin transcript]. Consistently, as new information emerges refuting the flow-survival hypothesis, the fish managers mount attacks on the data and its analysis in hopeless attempts to defend what has become the unsupportable foundation of their policies.

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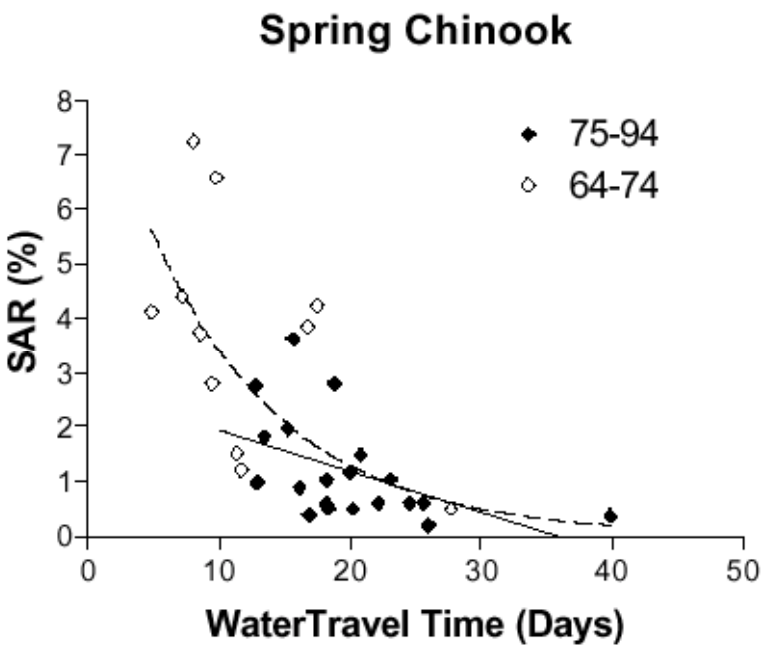

Figure 1. Regressions of smolt-to-adult returns versus water travel time for Snake River spring/summer chinook salmon for the 1964-1994 smolt migration (after Petrosky and Schaller 1998). The dashed line represents the regression line for the entire period; the solid line is for the years 1975-1994. From NMFS (2000b).

Table 1. History of Flow-Survival Relationship Key Studies and Program/Plans

Year	Evidence for flow-survival hypothesis and policy	Evidence against flow survival hypothesis and policy
1981	**Sims and Ossiander 1981** (73-79 Spring Chinook Studies)	
1983	**NPPC 1983** Fish & Wildlife Program* (**Policy**)	
1990	**CBFWA 1990** Integrated System Plan	
1992	**Petrosky 1992** (Adult Returns Rates Correlated with water Travel Time in Snake River)	**Marsh and Achord 1992** (First PIT-tag Study Shows High Survival with Low Flow)
1993	**Hilborn et al. 1993 ;** (Fall Chinook Flow-Travel Time Relationship) **Berggren and Filardo 1993** Snake River spring chinook travel time decreases with flow	
1994	**Cada et al. 1994** (Review from Several Systems Conclude Flow and Other Factors Affect Survival)	**Giorgi et al. 1994** (No Flow-Travel Time Relationship in mid-Columbia) **Olsen and Richards 1994** (Ocean Conditions affect West Coast Chinook)
1995	**NMFS 1995** BiOp* (Proposed Flow Targets) (**Policy**)	**Williams and Matthews 1995** (1970s, Low survival from Trash at Dams) **Skalski et al. 1996** (Fall Chinook Survival Depends on Comparison Stock)
1997		**Smith et al. 1997a** (1993-1997 Data Shows No Within-Year Flow Survival Relationship for Spring Chinook) **Giorgi et al. 1997 ; Smith et al. 1997b** (No Within-Year Flow Survival Relationship in Fall Chinook) **Mantua et al. 1997** (Ocean Regime Shifts Alter Salmon Production is an Alternative Reason for Stock Decline)
1998	**Marmorek et al. 1988** (FLUSH Passage Model Predicts Strong Flow Survival Relationship)	**Marmorek et al. 1988** (CRiSP Passage Model Predicts Weak Flow Survival Relationship) **Olsen et al. 1998** (Comprehensive Review of the Flow Program Questioning Policy, Hydrology, Biology, and Economics)
1999		**NMFS** obtains first estimate of smolt survival through the entire hydrosystem and requests FLUSH and CRiSP project survivals for model tests. FLUSH error is 3 times grater than CRiSP error.
2000	**NMFS 2000a** BiOp* (Continues with Flow Targets and Flow Augmentation Proposed in 1995 BiOP plus established a no net withdrawal policy) (**Policy**)	**NMFS 2000b** (No Flow Survival Relationship for Snake River Spring Migrants for 1995-1999) **NMFS 2000a** (NMFS Adapts SIMPAS Model in which Smolt Survival Depends on Distance, Not Travel Time) **Anderson et al. 2000; NMFS 2000b** (Snake River Fall Chinook Survival to LGR Dam Not Related to Travel Time, Survival has Highest Correlation with Release Date and Water Quality Parameters, which covary)
2001		**Muir et al. 2001** (Hatchery Chinook Survival Varied Inversely with Distance to LGR Dam. Hydrosystem Survivals in 1990S Equal Survivals in the1960s and Little Mortality Occurs in Reservoirs) **Williams et al. 2001** (Survival Increases from 1970s to 1990s not Accompanied by Change in Flow)

2002	Fisheries Agencies challenge the Giorgi 2002 report	**Giorgi et al. 2002** (Review of Data determined that little evidence for supporting flow survival relationship across water years 1993-2002 for yearling chinook and steelhead) **Smith et al. 2002** (Between Lower Granite and McNary Dam flow survival relationship with the in season or between years) **Anderson and Zabel *in review*** (Smolts pass a gauntlet of predators making survival dependent on distance not travel time)

* Fish migration and recovery programs.

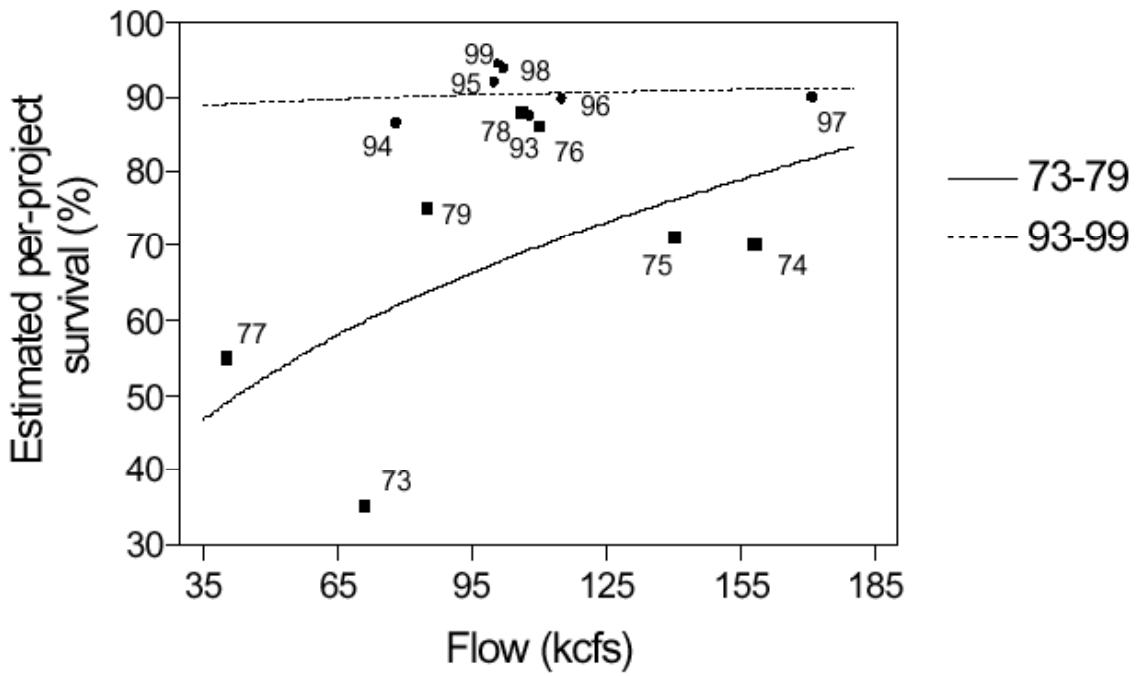

Figure 2. Historical and recent estimates of per-project survival (%) for yearling chinook salmon vs. index of Snake River flow (kcfs). Curves depict fitted nonlinear regression equations describing relationship between flow and survival in the two time-periods. Early period data from Raymond (1979) and Sims and Ossiander (1981). Graph from NMFS (2000b).

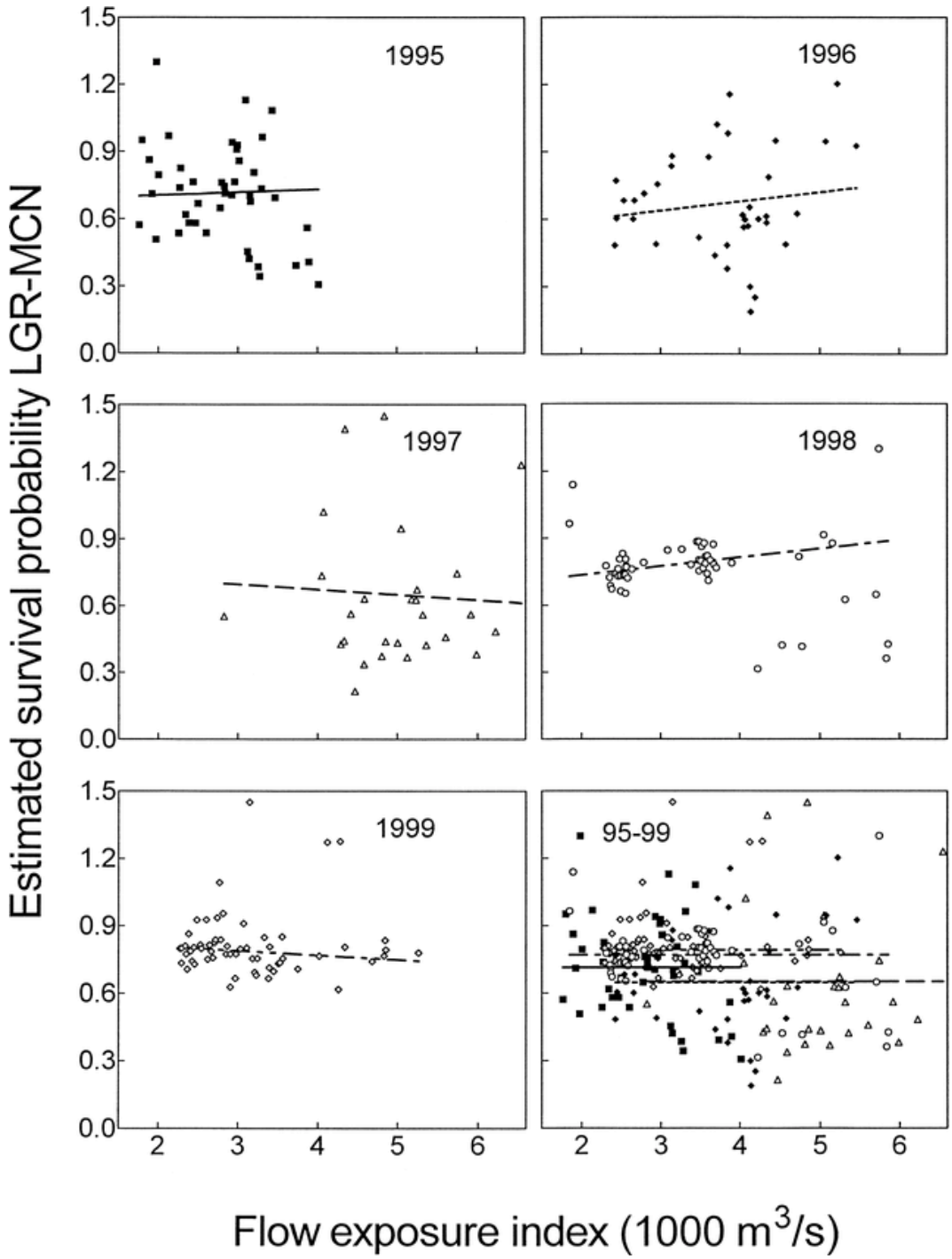

Figure 3. Relation between estimated survival from Lower Granite (LGR) Dam to McNary (MCN) Dam (d) and flow exposure index measured at Lower Monumental Dam for yearling chinook salmon, 1995–1999. Lines in the lower right panel depict the linear regression model identified in the model selection sequence. Regression lines are from weighted analysis (Figure from Smith et al 2002)

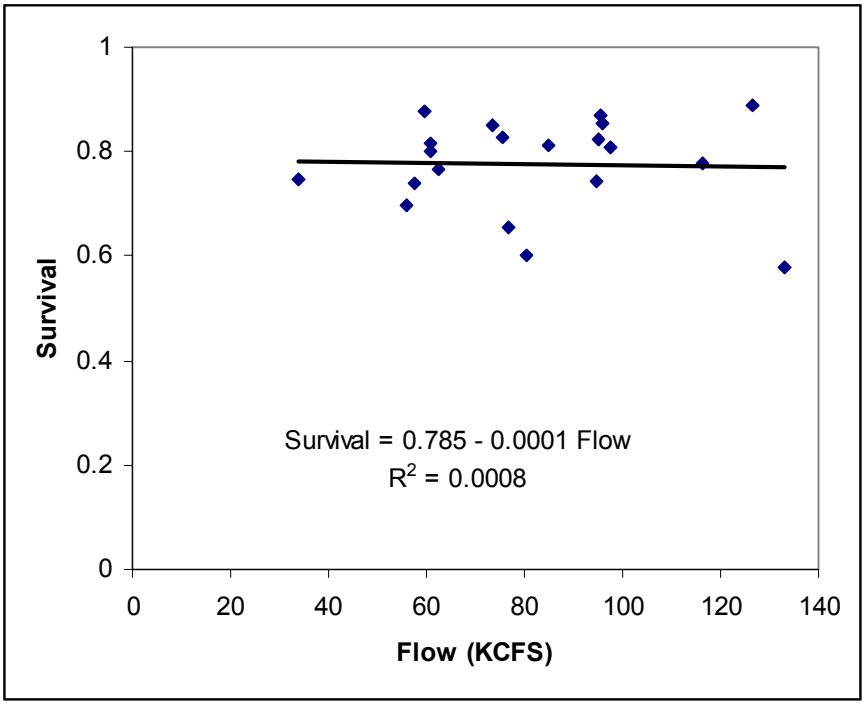

Figure 4. Relationship of flow to spring chinook smolt survival from Dworshak Hatchery to Lower Granite Dam for 10 years of PIT tag data from 1990-2001.

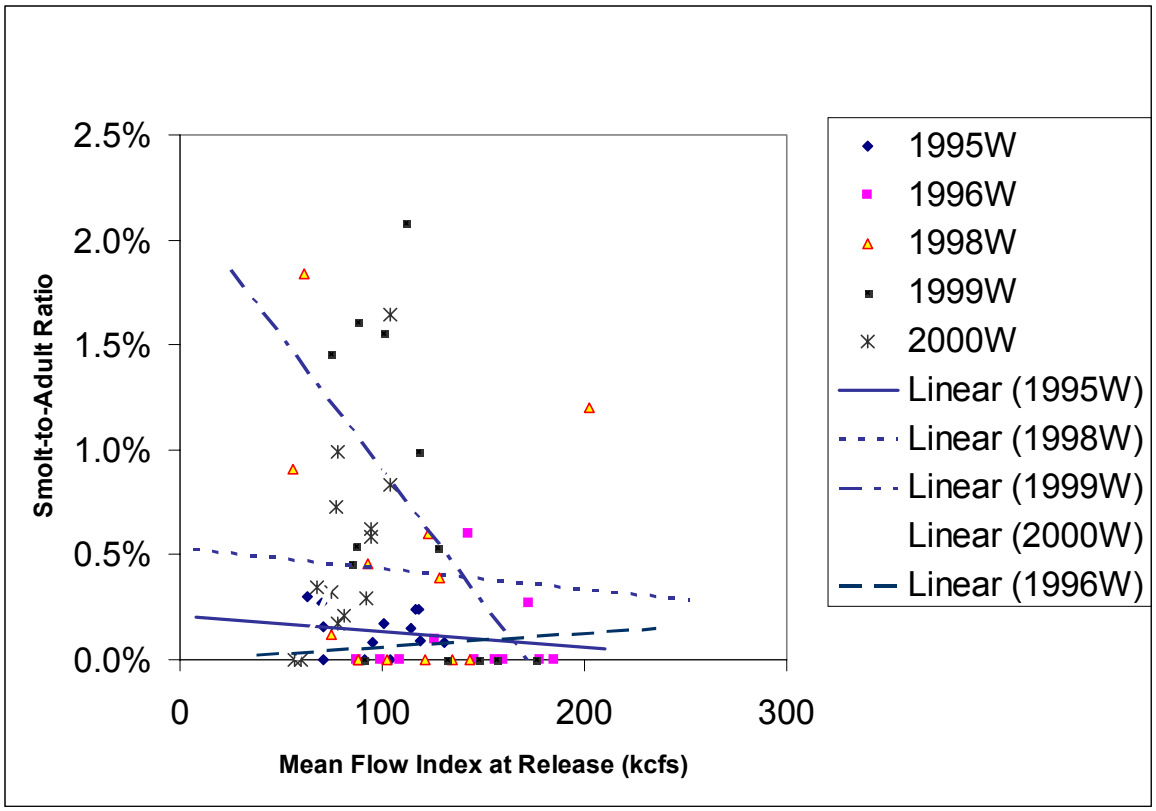

Figure 5. SAR vs. LGR flow index for PIT tagged spring chinook salmon tagged at Lower Granite Dam for between 1995 and 2000.

A collision theory based predator-prey model and application to juvenile salmonids in the Snake River Basin

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ABSTRACT

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 mortality depends mostly on distance traveled and only weakly on travel time. A new predator-prey model based on gas collision theory is proposed to reconcile 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 possibly explains the 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 velocity. Model coefficients estimated from mortality data of juvenile chinook salmon migrating through the tributaries of the Snake River are compared to independent estimates and are found to be in agreement.

Key words: predator-prey model; ecological neighborhood; reaction distance; mass action; gas collision theory; mean free path length; predator gauntlet; smolt migration; juvenile chinook salmon; Snake River; survival.

INTRODUCTION

In this paper, we adapt the mean-free path length model of molecular collisions to describe mortality events in predator-prey systems. The impetus for the approach is a set of observations showing the survival of juvenile salmon (smolts) migrating through the Columbia and Snake rivers is significantly related to the distance traveled but not travel time (Bickford and Skalski 2000, Muir et al. 2001, Smith et al 2002). At face value, this finding is perplexing, because from a first principles argument we expect that the mortality of migrating prey should increase with increased exposure to predators along the migration route. However, in these studies, fish traveling longer distances characteristically had higher mortality than fish that travel shorter distances irrespective of the travel time in either group. A modeling study of migrating juvenile salmon moving through a predator field, also in apparent contradiction to the observations, indicated that the mortality should increase as the downstream prey velocity decreases (Peterson and DeAngelis 2000). In a follow-up paper, DeAngelis and Peterson (2001) explored their model further and demonstrated that the mortality depended on the way in which the ecological neighborhood was formulated in their model, where the neighborhood is defined as the region within which an organism is active or has some influence during the appropriate period of time (Addicott et al 1987). Indeed, the importance of the scale at which predators and prey interact, "the ecological neighborhood," has been noted in many studies (Tilman and Kareiva 1997). In particular, predator-prey dynamics generated in individual-based models in which the predator-prey interactions are exactly defined cannot be reproduced in models using (mean-field) systems of differential equations (Pascual and Levin 1999). Furthermore, individual-based spatially explicit models show that the local movement of animals between sites can affect the synchrony of the large-scale population dynamics (Engen, Lande and Saether 2002). From these studies, we may be led to conclude that predator-prey systems are best studied with individual-based models that exactly define the ecological neighborhood and the interactions within it. However, while individual-based models can be more realistic, their interactions are complex and the model results may be extremely sensitive to the parameter estimations, and

therefore prone to error propagation (Levin 1992). Differential equation based predator-prey models, which are characterized by only a few parameters have value, because it is often possible to estimate the parameters from data. However, even though limited parameter models may fit data, do they correctly represent the ecological neighborhood, which is essential to modeling populations? Specifically, when varying the parameters in a differential equation model, which may or may not be calibrated to data, is the resulting response meaningful?

It is worth noting that most, if not all, models of predator prey interactions are based on the principle of "mass action" within the ecological neighborhood. For example, if C and F denote the number of predators and prey in an ecological neighborhood, and if the prey are equally vulnerable to predators in a time step, then the mass action assumption implies the number of prey eaten per unit time is proportional to the product of F and C, so predation rate ~ aFC (DeRoos et al. 1991), where a is a rate coefficient that may be constant or depend on other factors such as predator satiation as was assumed by Peterson and DeAngelis (2000). However, virtually missing in mass action models is the effect of predator and prey movements within the ecological neighborhood. Clearly, real behaviors in which the movements and distribution of predators and prey change in response to each other can significantly complicate the interactions and are likely to invalidate many assumptions in predator-prey models (Lima 2002). Overall then, the discrepancies between differing modeling approaches, between models and data, and between model assumptions and observed behaviors, are sufficient to reexamine the foundation of mass action predator-prey models.

In this paper, we reevaluate the predator-prey mass action assumption from first principles. Our goal is to derive a predator-prey law, in which an ecological neighborhood naturally evolves in terms of predator and prey movements, densities, and the field of perception.

SURVIVAL MODEL

The law of mass action in ecology has its origins in chemical theory derived in 1886 [1]. In the same way as a collision of two molecules produces one combined molecule, a predator and prey encounter produces one fed predator. However, the mean free path theory describing the collision of gases in terms of their velocity, size, and density provides a more fundamental description of an encounter. In particular, the concept of an ecological neighborhood naturally emerges from a description of predator-prey encounters in terms of collision. The mean free path length is derived through several similar approaches; here we follow an example illustrated by Feynman (Feynman, Leighton and Sands 1963).

Begin by assuming a prey takes an erratic but possibly directed path through its environment which contains predators distributed in an unspecified structured or random pattern and which may move about their environment. The average time between predator encounters is τ, and over an ensemble of prey and predator-prey interactions, assume that the probability of an encounter follows a Poisson distribution such that

1) $$\text{Chance of predator encounter} = \exp(-t/\tau)$$

where t is the total exposure time. To derive an expression for τ, first define the chance a prey encounters a predator in traveling a short distance by the equation

2) $$\text{chance of predator encounter in } dx = \frac{dx}{\lambda}$$

---

[1] P. Waage and C.M. Guldberg (1864) postulated the law of mass action based on experiments on esterification performed in 1862 by Berthelot and St Gillis. The law was introduced into the ecological literature by the great mathematician Vito Volterra (1926) who proposed to his future father-in-law and eminent hydrobiologist Umberto D'Ancona a mathematical model for D'Ancona's observations in which increases in some fish species coincided with decreases in others (Hutchinson 1978).

where λ is the prey's path length and dx is a short distance in the direction the prey travels.

The chance of encounter can also be expressed in terms of the predator density and a cross-sectional area α, within which a predator and prey must simultaneously reside in order for the predator to consume the prey. Consider α, or encounter area, a measure of the scale of the ecological neighborhood for predator prey interaction. Using the analogy to molecular collisions, how far a prey travels before encountering a predator depends on the number of predators, expressed as a predator density ρ, and the cross-sectional area at which a predator reacts to a prey. Now, moving the prey a distance dx defines a volume with a unit of area perpendicular to the direction of motion. Within this volume, there are ρdx predators (FIG. 1) and because the encounter area of each predator is α, the total predator encounter area within the unit area perpendicular to the prey's direction is $\alpha\rho dx$. The chance of encountering a predator is the total encounter area divided by the unit area, which is simply

3) $$\text{chance of predator encounter in } dx = \alpha\rho dx$$

Equating Eqs. (2) and (3) the path length is

4) $$\lambda = 1/\rho\alpha$$

The encounter time and path length are related by the u, which is prey velocity relative to the predator velocity. Thus, $\lambda = u\tau$ and the characteristic encounter time becomes

5) $$\tau = \frac{1}{\rho\alpha u}$$

This relative velocity, or encounter velocity, is expressed as a root-mean-squared (*rms*) relative velocity between the predator and prey as

6) $$u = \sqrt{E\left[(v-w)^2\right]}$$

where v is the absolute prey velocity and w is the absolute predator velocity. Next, represent predator and prey velocities in terms of average and fluctuating parts as

7) $$w = W + w^* \quad \text{and} \quad v = V + v^*$$

where W and V are the mean predator and prey velocities and w^* and v^* are the associated fluctuating or random velocities about the mean values (Sverdrup et al. 1942). By definition, the mean velocities are taken over the entire observation period so the fluctuation parts have zero mean values. The square of the encounter velocity in terms of its parts is

8) $$u^2 = V^2 - 2Vv^* + v^{*2} - 2VW - 2Wv^* + W^2 + 2Vw^* - 2v^*w^* + 2Ww^* + w^{*2}$$

The expected value of Eq. (8) simplifies as follows: Assume the fluctuating predator and prey velocities are uncorrelated and then, because by definition the means of the fluctuating parts are zero, all terms except the squared terms, have zero means. The *rms* encounter velocity defined by Eq. (6) reduces to

9) $$u = \sqrt{U^2 + \omega^2}$$

where the squared *mean* encounter velocity is

10) $$U^2 = (V - W)^2$$

and the mean squared *random* encounter velocity is

11) $$\omega^2 = E\left[v^{*2}\right] + E\left[w^{*2}\right]$$

Note that ω^2 is the sum of the variances of the predator and prey velocities.

Using Eq. (9) in Eq. (5) to define τ in Eq. (1) the prey survival as a function of time is

12) $$S = \exp\left(-\frac{t}{\lambda}\sqrt{U^2 + \omega^2}\right)$$

Special cases of the survival model

Several special cases arise from Eq. (12). If the predators are resident within a habitat then by definition $W = 0$. If the prey migrate through the habitat the migration distance is defined $x = Vt$, where t is the migration travel time and the survival is a function of migration distance and time as

$$S = \exp\left(-\frac{1}{\lambda}\sqrt{x^2 + \omega^2 t^2} \right) \tag{13}$$

Equation (13) will be referred to as the XT model. Further, if the prey migration is fast and the predators are resident and nearly stationary then $V^2 \sim U^2 >> \omega^2$ and prey survival becomes a function of distance

$$S = \exp\left(-x/\lambda\right) \tag{14}$$

Equation (14) will be referred to as the gauntlet model. The general model admits two special cases in which prey survival depends only on the amount of time prey are exposed to predators. If the prey are stationary, so $v = 0$, and predators are resident or migratory, then the prey survival equation becomes

$$S = \exp\left(-w_{rms} t/\lambda\right) \tag{15}$$

where w_{rms} is the root mean squared predator velocity. If the predators and prey are both mobile and resident within the habitat so $U^2 = 0$, then

$$S = \exp\left(-\omega t/\lambda\right) \tag{16}$$

A CASE STUDY WITH MIGRATING JUVENILE SALMON

Studies of juvenile chinook salmon migrating through the Snake and Columbia River system indicate survival depends primarily on distance, not travel time (Muir et al. 2001, Smith et al. 2002). Predator prey models based on mass action are in conflict with this finding because in such models survival should depend on travel

time. However, the XT model has distance dependent survival so it is instructive to fit the model to the salmon migration data. We use mark recapture studies conducted on Snake River system. Between 1993 and 1998, 78 tagged groups of fish were released from 17 hatchery locations in the tributaries of the Snake River Basin (FIG. 2). The fish were tagged with passive integrated transponder (PIT) tags (Prentice, Flagg, and McCutcheon 1990) and were released from locations in the Snake River tributaries ranging from 61 km to 772 km upstream of the detection site at Lower Granite Dam. Release sample sizes ranged from 135 to 27,527 fish. Survivals to Lower Granite Dam were estimated with the multiple–recapture model for single-release groups (See Muir et al. 2001). Muir et al. (2001) noted the estimated survival from the hatcheries was inversely correlated with migration distance to Lower Granite Dam (r^2 =0.64, P< 0.001). Survival also had a weak inverse relationship with travel time to Lower Granite Dam (r^2 = 0.17, P > 0.07).

To test the model with the Muir et al. (2001) data, assume the predators are resident in the Snake River tributaries. Therefore, Eq. (13) should be an appropriate descriptor of the juvenile salmon survival. To estimate the model parameters, Eq. (13) is written in the multiple-linear form

17) $$(\log S)^2 = ax^2 + bt^2$$

where the model parameters are defined

18) $$\lambda = 1/\sqrt{a} \quad \text{and} \quad \omega = \sqrt{b/a}$$

Because of the large difference in sample sizes, we weighted the individual survival estimates by one over the square of the sample size from each release site. We performed the regressions for each year and for the combined years (Table 1). Using the estimated parameters and the range of parameter errors, the mean, minimum, and maximum values of the λ and ω were estimated using Eq. (18) (Table 2).

RESULTS

The r-squares of the fit of the gauntlet model (Table 1) are all above 0.6. Considering the regressions for the individual years, in all years except 1997 the p-value on the *a* coefficient is highly significant. For the *b* coefficient, only 1997 is significant while the values in the other years have standard errors equal to or greater than the parameter estimate. For the regression on the combined years, the *a* coefficient is highly significant and the *b* coefficient is significant but less so. The estimated mean path length is between 400 and 900 km for all years except 1997, which is considerably larger (Table 2). In most years because the *b* coefficient is negative, the random encounter velocity ω can not be calculated. However, because the *b* coefficients are not statistically different from zero in all years except 1997, we may assume that ω is very small but positive for this data. Thus, the random encounter velocity is near zero.

However, 1997 is anomalous and needs to be reconciled with the other years. A recorded high flow occurred in 1997, but surprisingly fish travel times were some of the longest observed in the six years of study, suggesting that the flood delayed smolt migration and resulted in that year having a predator-prey dynamic different from the other years. For all years combined, the random encounter velocity is 9.5 cm/s and the mean smolt path length is 745 km (Table 2). Excluding 1997, the mean path length is 500 km and the random encounter velocity is zero. In comparison, from the observed migration times and distances to Lower Granite Dam, the average smolt migration velocity was 14 cm/s. Thus, if the encounter velocity is on the order of a few cm/s, then from Eq (9) the squared average migration velocity ($V^2 = 196$) dominants the random component ($\omega^2 = 1$) and the survival should depend mostly on travel distance as was reported by Muir et al. (2001).

COMPARISON WITH INDEPENDENT PREDICTIONS

In this section, we compare parameters estimated from the XT model to estimates derived from other methods using independent observations.

Encounter distance

From Eq. (4), the predation encounter distance, δ, characterizing the average distance at which a predation event occurs can be defined

$$\delta = 1/\sqrt{\pi\rho\lambda} \tag{19}$$

To estimate δ, the predator density over the migration path is required. To derive a very approximate estimate of ρ, we use population estimates of northern pikeminnow and smallmouth bass, which are the major predators of juvenile salmon in the river (Poe et al. 1991, Knutsen and Ward 1999). Estimated populations for Lower Granite Reservoir are 26,000 northern pikeminnow larger than 250 mm (*public communication*[2]) and 20,911 smallmouth bass larger than 174 mm (Bennett et al. 1997). Dividing the combined populations by the volume of Lower Granite Reservoir, 597 $\times 10^6$ m^3, the predator density is $\rho = 7.9 \times 10^{-5}$ predators m^{-3}. Then, using the range of model estimates of λ, the predator-prey encounter distance is about 9 cm with a minimum of 1.6 cm for 1997 and a maximum of 10.5 cm for 1995. The corresponding encounter areas are $\alpha = 8$, 254 and 352 cm^2 receptively. Because λ is derived from survival estimates of fish migrating for several weeks, the encounter distance represents an average of day and night conditions over the migratory period.

For an independent estimate of the encounter distance, consider observations of predator reaction distance, which should be somewhat greater than the encounter distance because reaction distance identifies the distance at which a predator first reacts to a prey while the encounter distance, by definition, is the distance within which a predation event occurs. Reaction distance depends on water clarity and light level (Vogel and Beauchamp 1999). In 1997, the water clarity based on horizontal secchi disk readings in the Grande Ronde, a tributary of the Snake River, ranged

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[2] National Marine Fisheries Service. 2000. Salmonid travel time, and survival related to flow in the Columbia River Basin. URL: <http://www.nwfsc.noaa.gov/pubs/white/whiteflow.pdf>.

between 20 and 100 cm, with a mean of about 50 cm (Steel 1999). This equates to a turbidity reading of about 40 NTU (Steel and Neuhauser 2002). Additionally, secchi reading in Lower Granite Reservoir typically vary between 10 and 50 cm[3]. Using the Vogel and Beauchamp (1999) reaction distance formula for the response of lake trout to rainbow and cutthroat trout prey, the reaction distance is 37 cm under midday conditions (100 lux) and a turbidity of 40 NTU, while in a midcrepuscular period (0.17 lux) the reaction distance is 5 cm. Additionally, note that laboratory studies on brook trout (Sweka and Hartman 2001) and rainbow trout (Barrett, Grossman, and Rosenfeld. 1992) found reaction distances less than 20 cm for turbidity levels greater than 30 NTUs. Furthermore, because the reaction distance is zero at night, the reaction distance averaged over the day should be about half the midday values and thus between 10 and 20 cm.

Thus, the 9 cm encounter distance derived from the XT model is reasonable because it is close to but less than the reaction distances estimated above. Consequentially, we may expect that in the Snake River tributaries, as has been found in other systems (Gregory and Levings 1998), water visibility is an important determinant of predator-prey encounter distance and therefore of smolt survival.

Random encounter velocity

The predator-prey random encounter velocity depends on the random prey velocity, v^*, and the random predator velocity, w^*, according to Eq. (11). An upper estimate of v^* can be derived from Zabel (2002) in which the distribution of smolt migration travel times was modeled with an advection-diffusion equation controlled by two parameters: migration velocity, r, and a spread term, σ^2. The travel time distribution is inversely related to the migration velocity distribution and, based on Tweedie (1957), the variance in the migration velocity is

[3] Columbia River DART. 2002. URL: <http://www.cbr.washington.edu/dart/>.

20) $$Var(x/t) = \frac{r}{x}\sigma^2 + \frac{2}{x^2}\sigma^4$$

where x is the migration distance. The square root of Eq. (20) provides an upper estimate of v^*. From four years of data on wild Snake River spring chinook migrating 233 km from the Salmon River to Lower Granite Dam $\sqrt{Var(x/t)}$ ranged between 9.0 and 16.1 cm/s.

For a second measure of the encounter velocity, consider predator velocities determined from radio-tagged Northern pikeminnow in John Day Reservoir. Using fish positions determined several times per day in May 1993 and 1994, average velocity was 7 cm/s in the tailrace and 1 cm/s in mid-reservoir (Martinelli and Shively 1997, Martinelli, Shively, and King 1993). Additionally, the coefficients of variation were about one in both areas so the random velocity about equals the average velocity, and to a first order the predator random velocity is expected to be a few cm/s.

In comparison, the XT model estimated encounter velocity for the Snake River tributaries range between 0 and 287 cm/s, and (excluding 1997) the encounter velocity ranges between 0 and 11.1 cm/s. Although these estimates are relatively close, a direct comparison between them is problematic. First, uncertainty in all estimates is large and it is not possible to put meaningful confidence intervals on any of them. Second, the estimates derived from prey and predator movements only represent components of the combined estimate of the XT model. Third, the prey random velocity estimated from Eq. (20) contains additional elements other than the actual random swimming velocity. Equation (20) is derived from a difference in arrival times of fish after traveling the distance x. Because early in migration smolts mostly migrate at night and are presumed to hold station near the bottom during the day (Zabel 2002), the spread in a release group's arrival time at a downstream location is the result of both their actual random swimming velocity and their diel station holding behavior. Thus, the velocity derived from Eq. (20) should represent an upper limit of v^*. Considering these caveats, XT model's estimate of ω near zero is reasonable.

DISCUSSION

The initial impetus for this model was the consistent result from many studies that the survival of juvenile spring/summer chinook migrating through the Snake and Columbia Rivers was essentially independent of smolt travel time and flow (Bickford and Skalski 2000, Muir et al. 2001, *public communication*[4]). However, several studies also found that survival was a function of the migration distance. In particular, the survival of hatchery fish from Snake River tributaries to Lower Granite Dam were significantly related to distance traveled, but not travel time (Muir et al. 2001). Because classical predation theory based on mass action fails to explain these observations, we reconsidered the predator-prey dynamics from first principles gas collision theory. We developed a model in which prey survival depends on the mean and random encounter velocities between predators and prey, a predator-prey encounter distance, and predator density.

The relative contributions of travel time, T, and travel distance, X, on prey survival depends on the random predator-prey encounter velocity. When this velocity is small, predators are relatively stationary and prey move more or less directly through their habitat. Under this scenario, once a prey passes a predator, future encounters are unlikely: prey essentially traverse a gauntlet of predators and so mortality depends on the number of predators passed, which functionally depends on migration distance, not migration time. When the random encounter velocity is large, predators and prey move about the habitat; multiple encounters can occur and so the prey mortality rate depends on their exposure time to predators.

The XT model illustrates that the relationship between the total migration time, distance, and survival depends on small-scale ecological neighborhood of predator and prey interactions. A model missing the essentials of these interactions can produce erroneous large-scale features. For example, neither a simple model with survival

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[4] NMFS. 2000. URL;<http://www.nwfsc.noaa.gov/pubs/white/whiteflow.pdf>.

declining exponentially in time, nor an individual based, finite cell model in which mortality depends on cell residence time (e.g., Peterson and DeAngelis 2000) decouples the effects of distance and time on survival. The small-scale predator-prey interactions, which in the XT model produce the gauntlet effect, are missing in both models. However, the XT model's characterization of small-scale interactions is very simple. Missing are any considerations of predator-prey bioenergetics or fish responses to their immediate environment, which is on the order of centimeters. Incorporating these factors should provide additional valuable insights into predator-prey dynamics.

Using XT model we are able to compare the encounter distance and encounter velocity to estimates made with independent data using other approaches. The encounter distance is similar to the reaction distance and is approximately equal to the water clarity. The encounter distance estimated by the model is in good agreement with measurements of water clarity for the Snake River and for laboratory estimates of reaction distance. Although estimates of encounter velocities are only available indirectly for smolts, estimates derived by two methods are reasonably close to the model estimated encounter velocity. Thus, agreement between model and independently parameter estimates is encouraging. Perhaps more importantly though, in the same fashion that gas collision theory provided detail and enumeration to the law of mass action in chemistry, the XT model provides an expanded and intuitive framework in which to describe the predator-prey ecological neighborhood. In particular, the theory provides a simple coupling between small-scale predator-prey interactions and large-scale patterns.

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Tables

Table 1. Survival equation coefficients for spring chinook hatchery releases and migration to Lower Granite Dam. Regressions for years 1993-1998 and all years (All) are based data in (Muir et al 2001) with Eq. (17).

		a parameter			*b* parameter		
year	r-sq	Value 10^{6}	Std err 10^{6}	p-val	Value 10^{4}	Std err 10^{4}	p- val
1993	0.829	3.381	0.665	0.0005	-1.192	1.537	0.455
1994	0.939	3.707	0.308	<0.0001	-1.220	1.107	0.288
1995	0.687	5.981	1.587	0.0021	-2.304	3.987	0.572
1996	0.647	4.477	1.356	0.0057	-1.949	2.110	0.372
1997	0.853	0.005	0.885	0.9961	3.803	1.172	0.022
1998	0.923	1.209	0.347	0.0059	0.505	0.548	0.378
All	0.603	1.803	0.423	0.0001	1.636	0.642	0.012
w/o 1977	0.632	4.010	0.499	<0.0001	-2.20	0.91	0.019

Table 2. model parameter ranges. λ has units of km, ω has units of cm/s. Subscripts min and max are defined by standard errors on the regression parameters.

Year	λ_{min}	λ_{ave}	λ_{max}	ω_{min}	ω_{ave}	ω_{max}
1993	497	544	607			3.6
1994	499	519	542			
1995	364	409	477			6.2
1996	414	473	566			2.3
1997	1060	14759		17.2	287.8	
1998	802	909	1077		6.5	11.1
All	670	745	851	6.7	9.5	12.8
w/o 1977	471	499	534			

Figure Captions

FIG. 1. Illustration of a prey moving a distance *dx* through a unit area of predator habitat.

FIG. 2. Map showing Snake River tributaries and the hatcheries from which fish were released for survival studies.

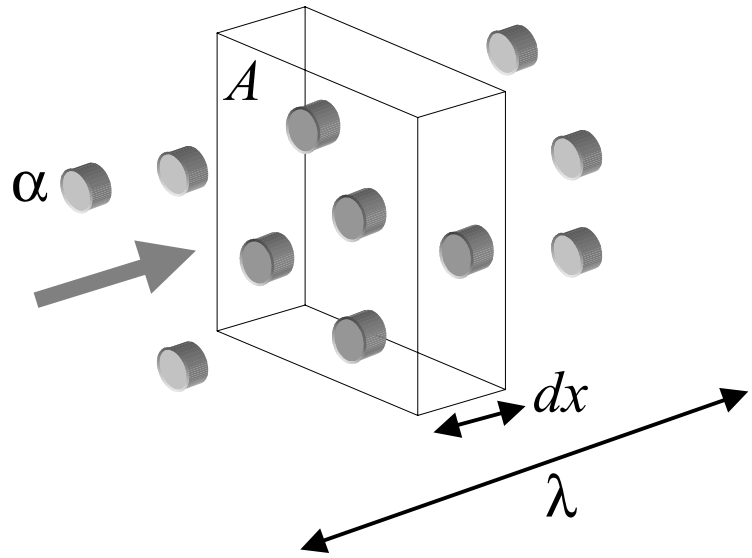

Figure 1

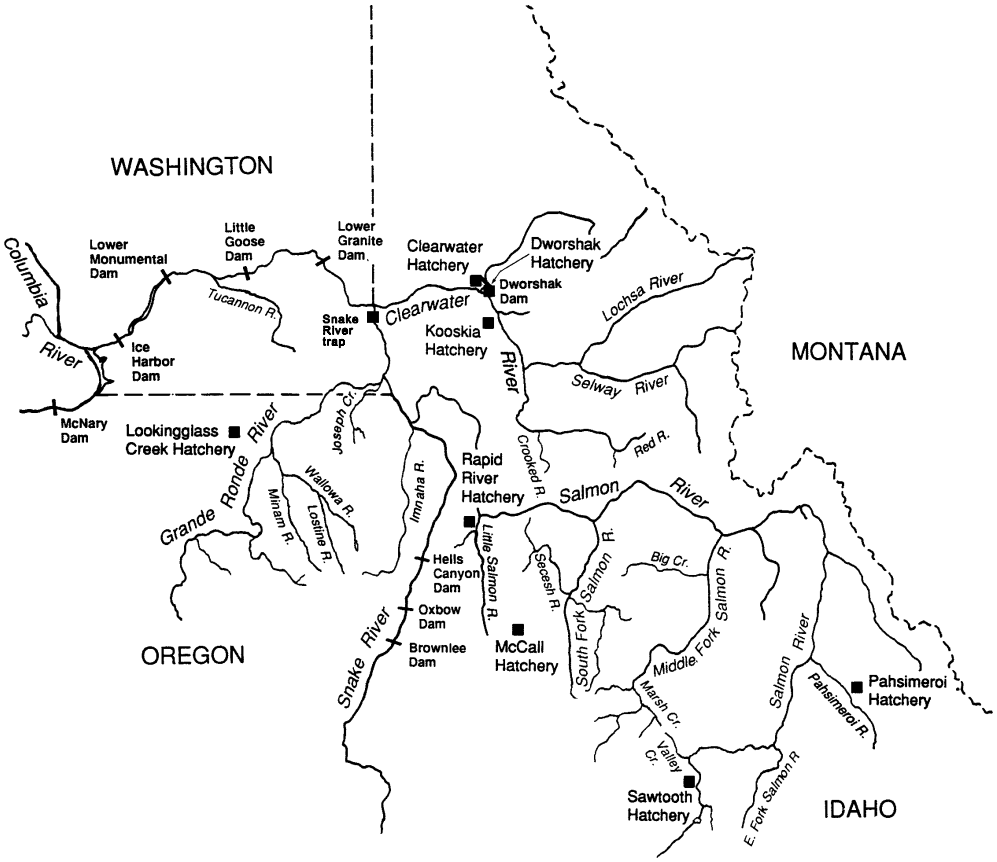
WASHINGTON
MONTANA
OREGON
IDAHO
Columbia River
Lower Monumental Dam
Little Goose Dam
Lower Granite Dam
Tucannon R.
Snake River trap
Clearwater
Clearwater Hatchery
Dworshak Hatchery
Dworshak Dam
Lochsa River
Kooskia Hatchery
Ice Harbor Dam
McNary Dam
Selway River
Lookingglass Creek Hatchery
Grande Ronde River
Joseph Cr.
Wallowa R.
Minam R.
Lostine R.
Imnaha R.
Rapid River Hatchery
Crooked R.
Red R.
Salmon River
Little Salmon R.
Hells Canyon Dam
Oxbow Dam
Brownlee Dam
Snake River
McCall Hatchery
Secesh R.
South Fork Salmon R.
Big Cr.
Middle Fork Salmon R.
Marsh Cr.
Valley Cr.
Sawtooth Hatchery
Salmon River
Pahsimeroi Hatchery
Pahsimeroi R.
E. Fork Salmon R.

Figure 2

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.

Table of Contents

Introduction 4

Survival Model 5

Theory 5

Fitting the model to data 10

Data 12

Analysis 13

Survival through the hydrosystem 14

Chinook survival in the hydrosystem 14

Steelhead analysis 28

Survival through Snake River tributaries 30

Snake River spring chinook 30

Snake River fall chinook 35

Snake River steelhead 39

Survival and water transit time 43

Summary 47

XT-model implications to flow management 49

Literature Cited 52

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

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

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

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.

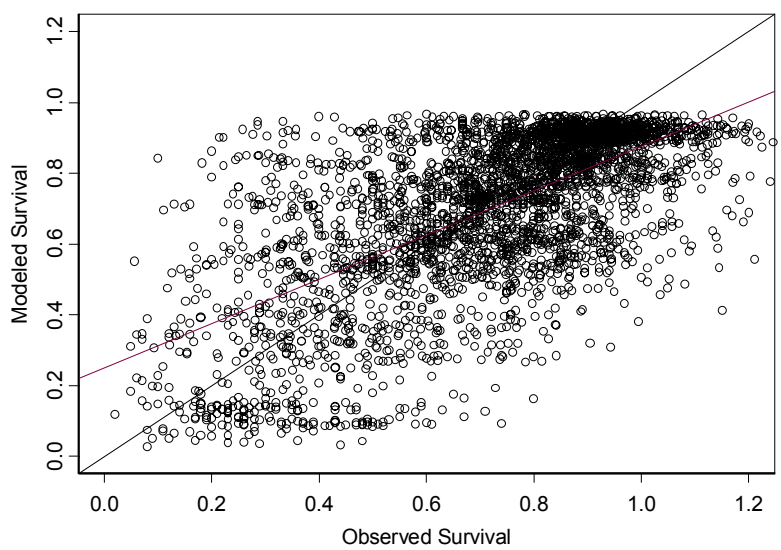

Figure 1. Observed vs. XT-model survival for chinook migration between LGR and MCN dams over the years 1995-2002. Includes all data with weight > 10.

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

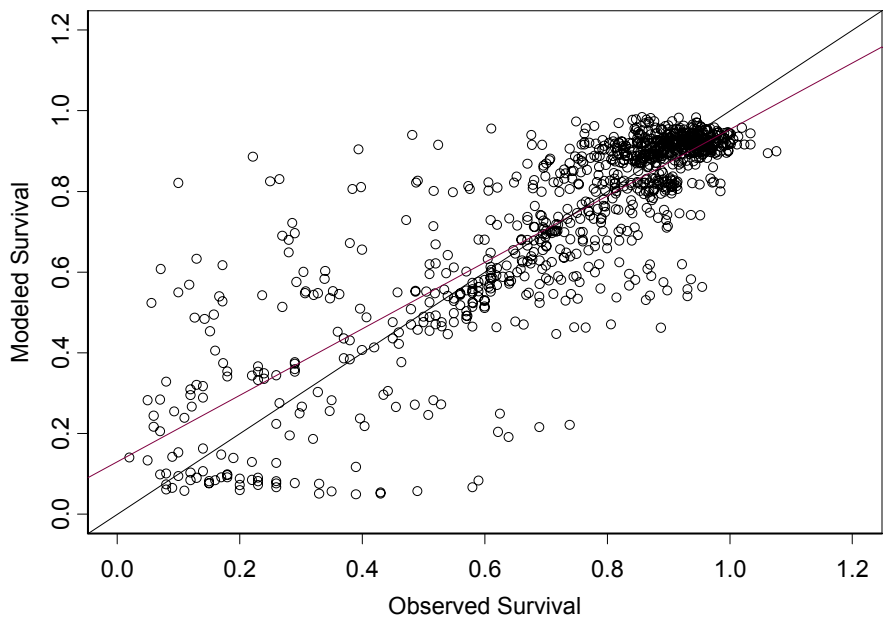

Figure 2. Observed vs. X-model survival for chinook migration between LGR and MCN over the years 1995-2002. Includes all data with weight > 200.

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.

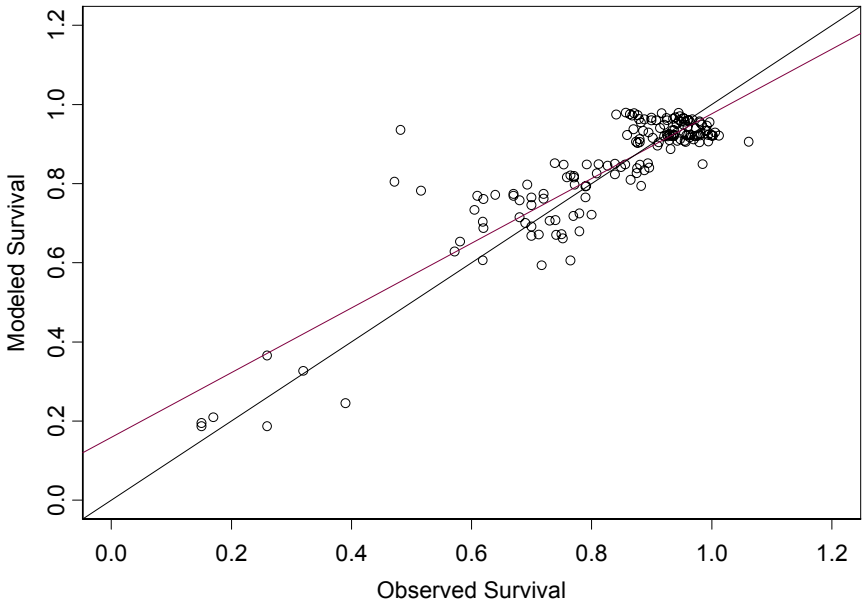

Figure 3 Observed vs. X-model survival for chinook migration between LGR and MCN dams in 2002. Includes all data with weight > 200.

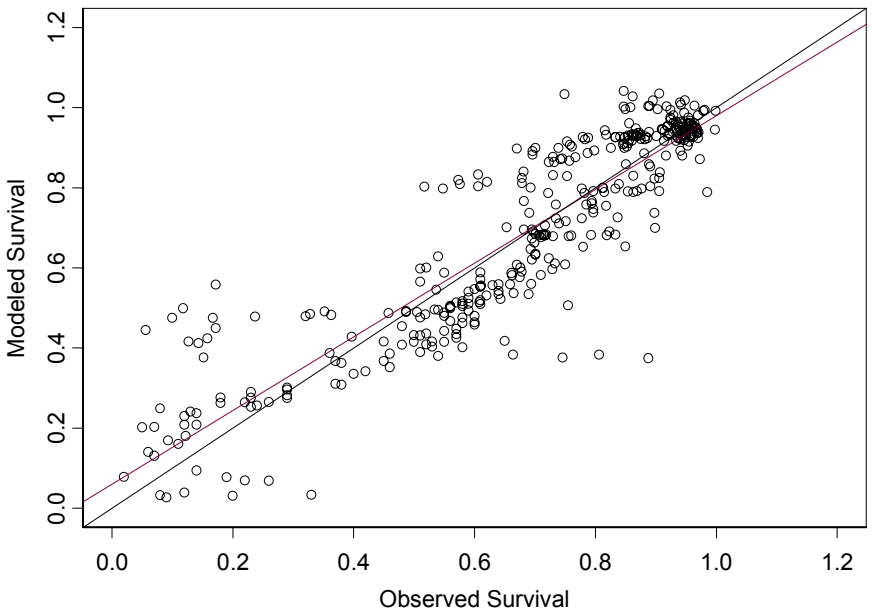

Figure 4 Observed vs. X-model survival for chinook migration between LGR and MCN dams in 2001. Includes all data with weight > 200.

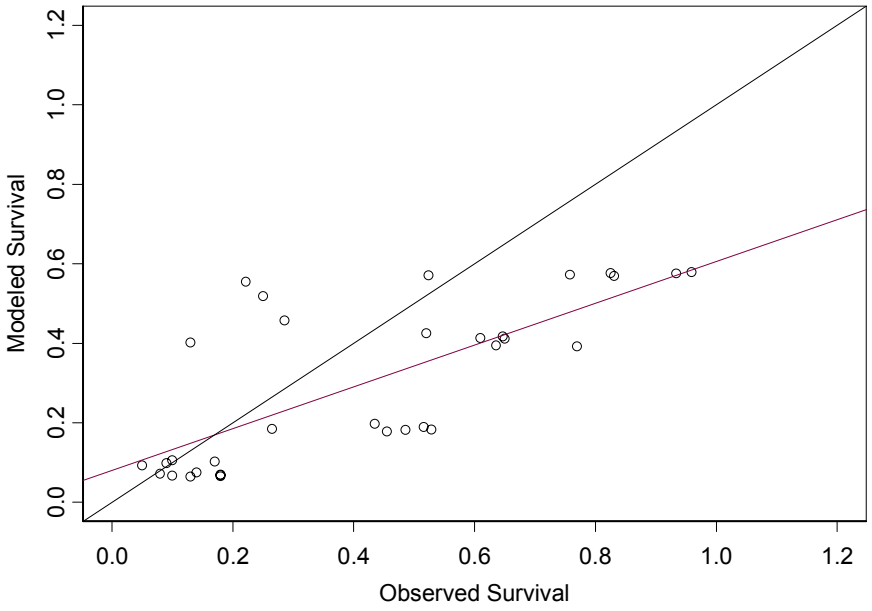

Figure 5. Observed vs. X-model survival for chinook migration between LGR and MCN dams in 1997. Includes all data with weight > 200.

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.

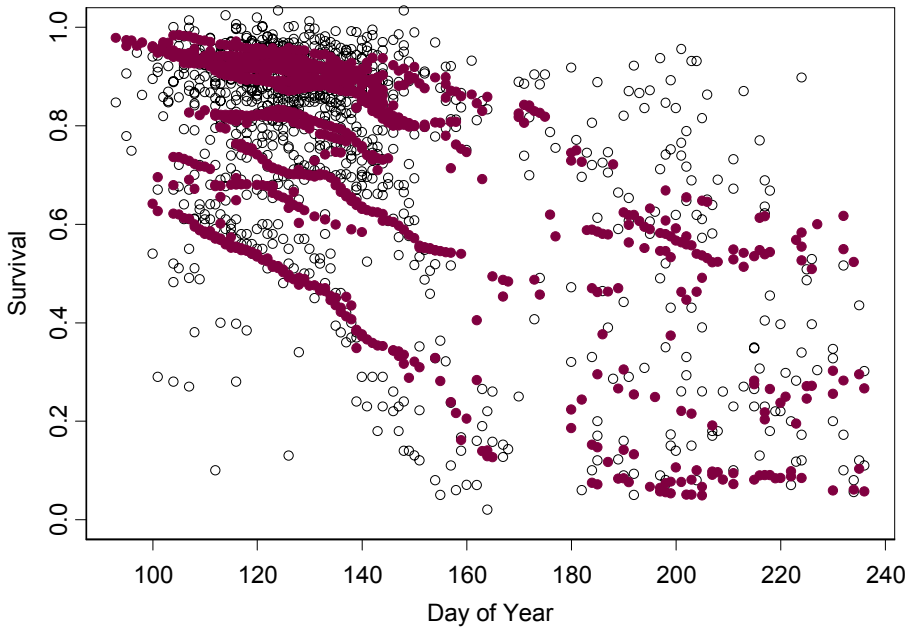

Figure 6. Modeled and observed chinook survival vs. day of the year over single and multiple reaches between LGR to MCN over the years 1995-2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

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.

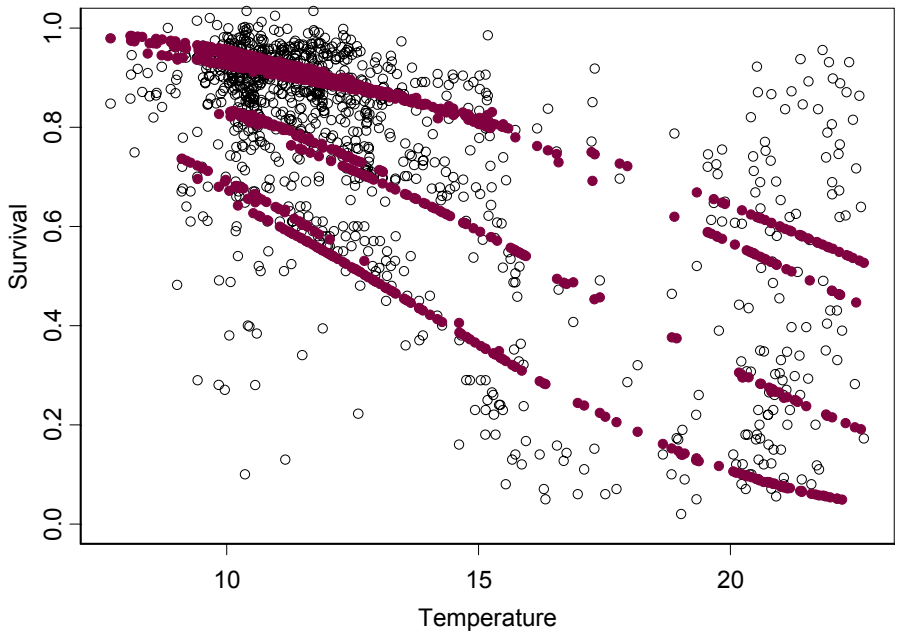

Figure 7. Modeled and observed chinook survival vs. temperature (^{o}C) over single and multiple reaches between LGR to MCN over the years 1995-2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

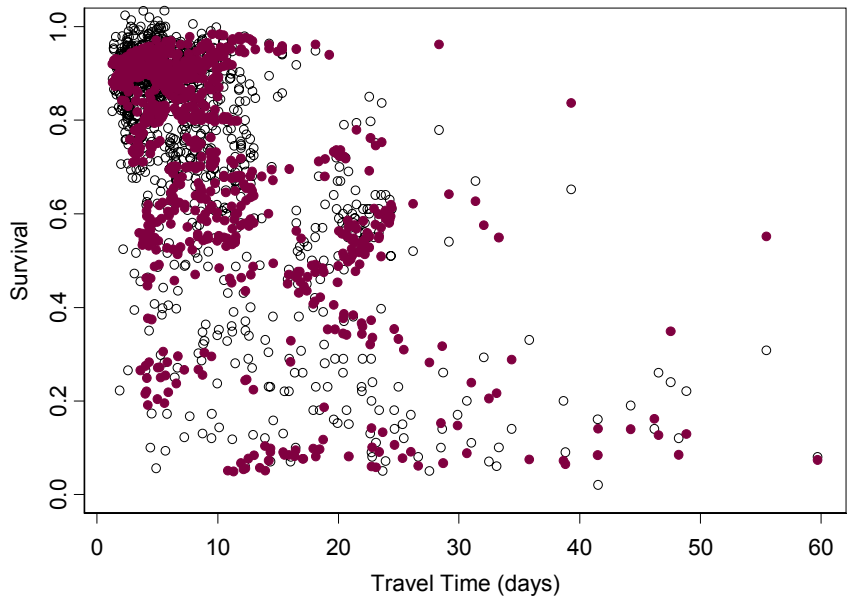

Figure 8. Modeled and observed chinook survival vs. travel time over single and multiple reaches between LGR to MCN over the years 1995-2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

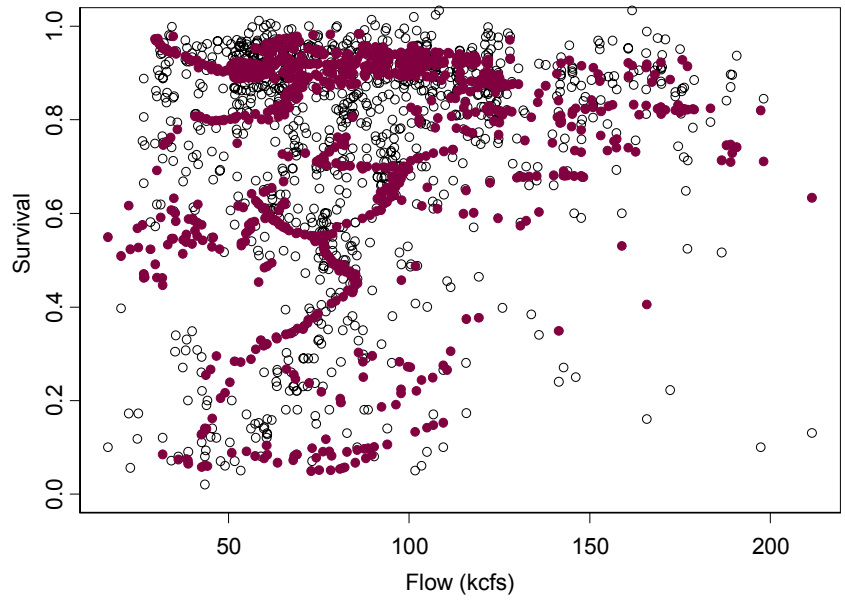

Figure 9. Modeled and observed chinook survival vs. flow over single and multiple reaches between LGR to MCN over the years 1995-2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

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.

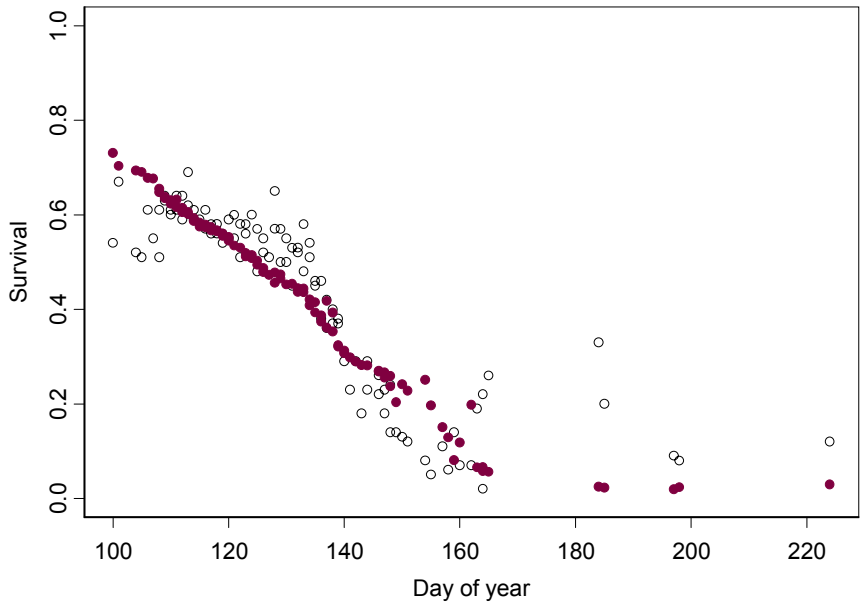

Figure 10. Modeled and observed chinook survival vs. day of the year for migration between LGR and MCN in 2001. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

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.

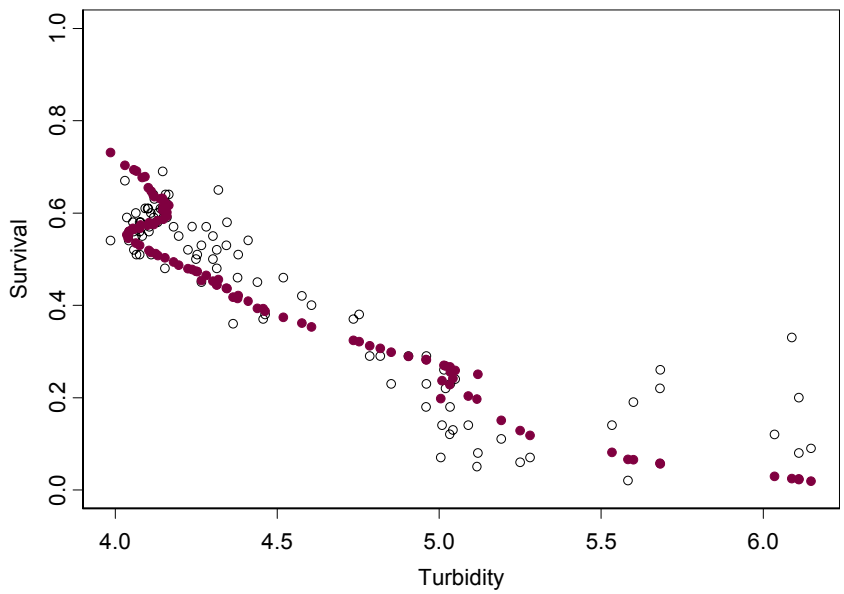

Figure 11. Modeled and observed chinook survival vs. turbidity (ft) for migration between LGR and MCN in 2001. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

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.

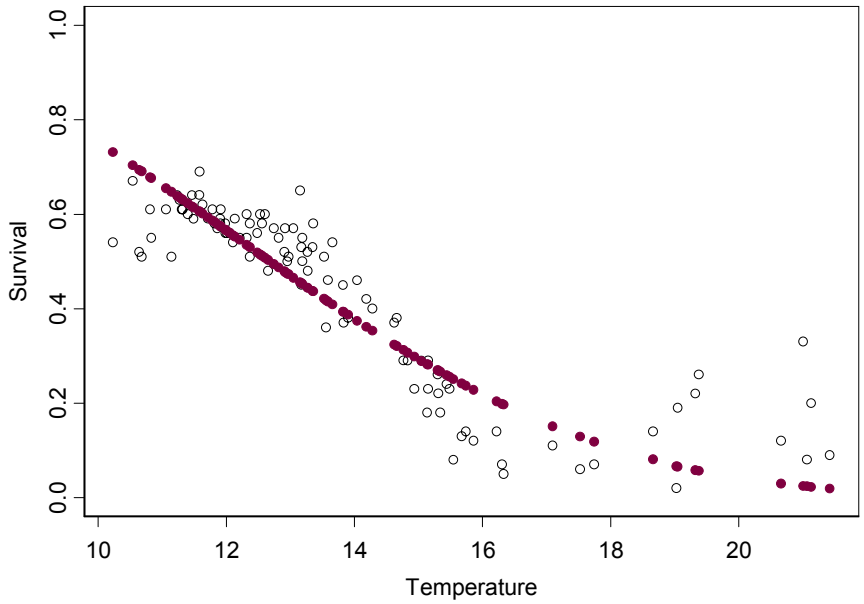

Figure 12. Modeled and observed chinook survival vs. temperature (^{o}C) for migration between LGR and MCN in 2001. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

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.

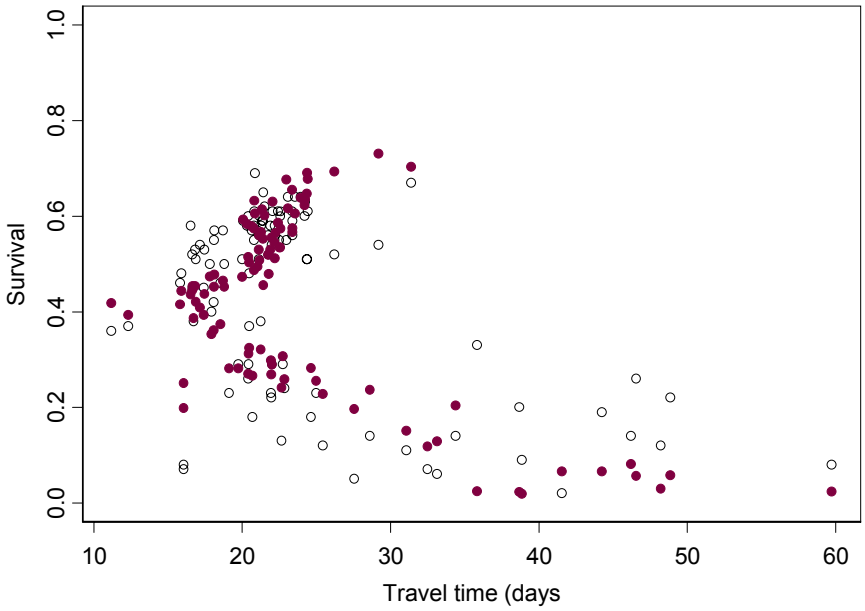

Figure 13. Modeled and observed chinook survival vs. travel time for migration between LGR and MCN in 2001. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

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.

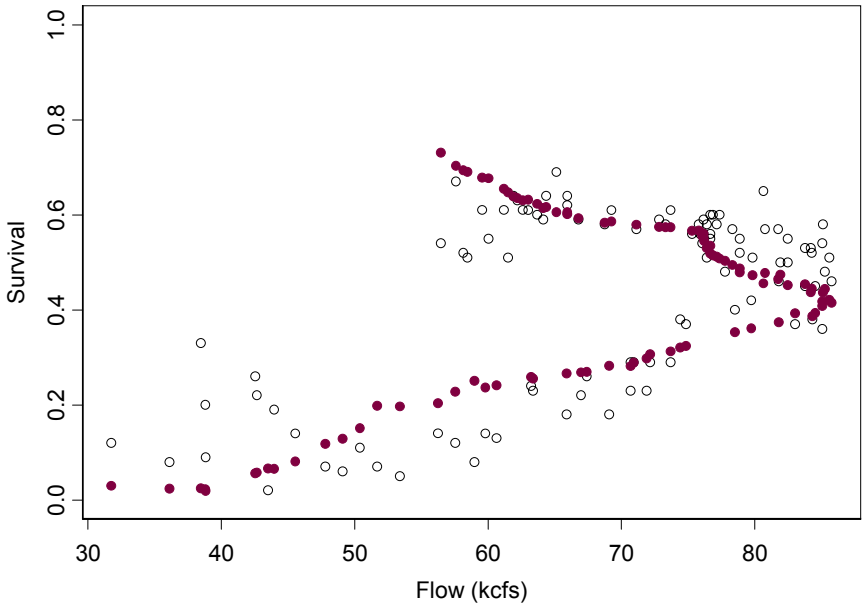

Figure 14. Modeled and observed chinook survival vs. flow for migration between LGR and MCN in 2001. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

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.

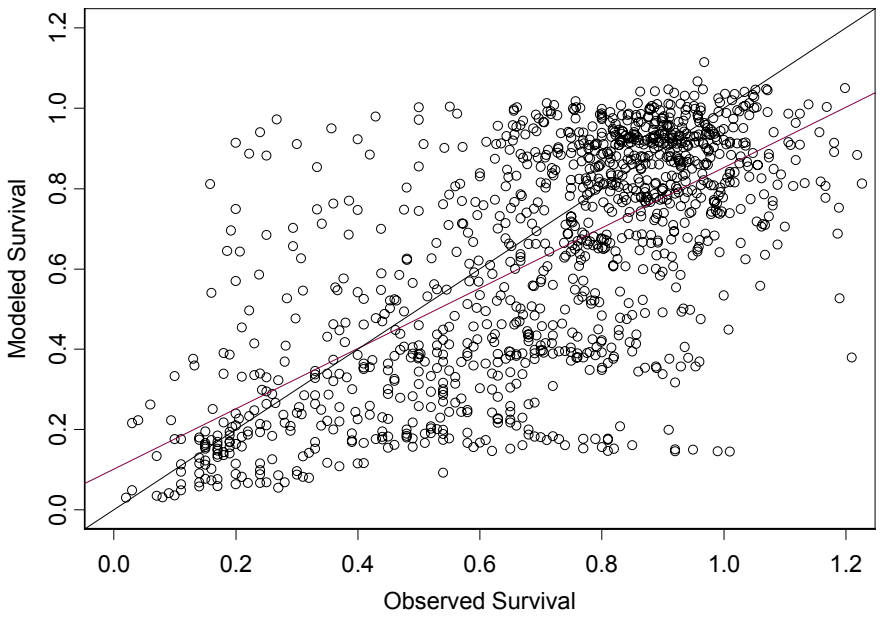

Figure 15. Observed vs. X-model survival for steelhead migration between LGR and MCN dams over the years 1995-2002 based on 1185 data points with a weighting factor > 10.

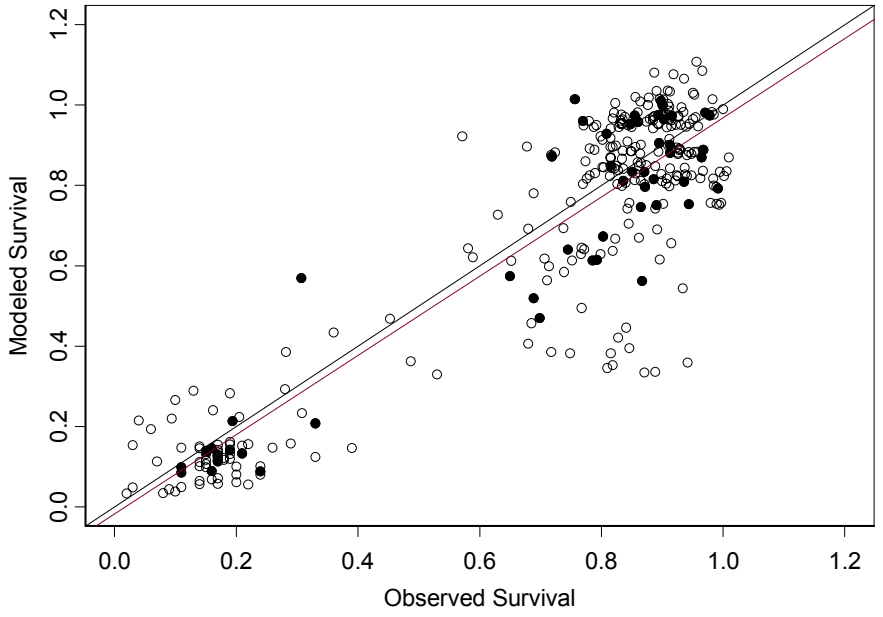

Figure 16. Observed vs. X-model survival for steelhead migration between LGR and MCN dams over the years 1995-2002 based on 315 data points with a weighting > 200. The solid dots represent 2001 data.

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).

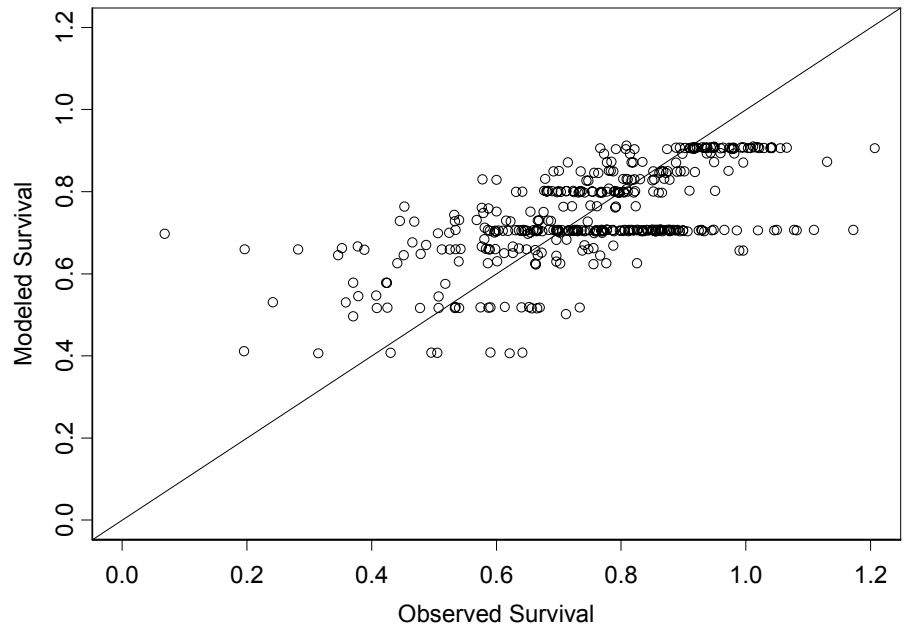

Figure 17. Observed vs. X-model survival for hatchery spring chinook migration between the hatchery release points and LGR Dam over the years 1995-2002 based on 400 data points with no weighting.

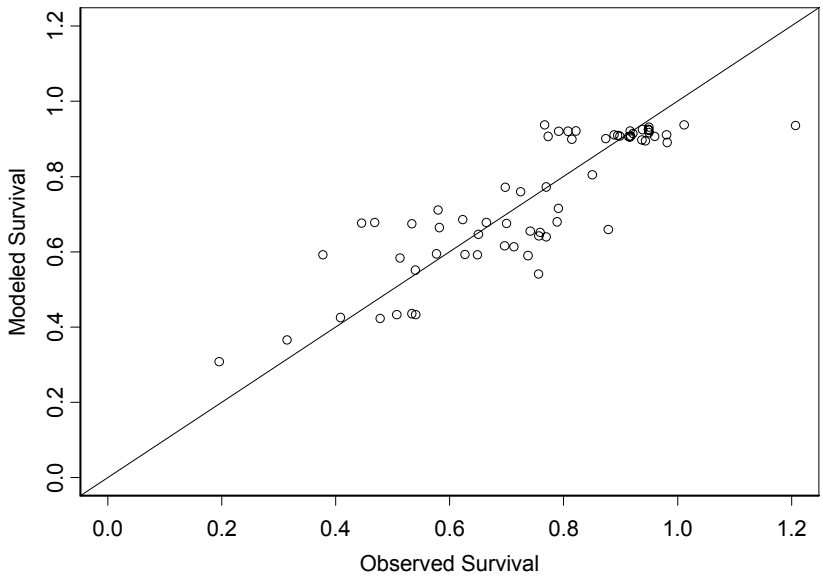

Figure 18. Observed vs. X-model survival for hatchery spring chinook migration between the hatchery release points and LGR Dam for 1995 based on 62 data points with no weighting.

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.

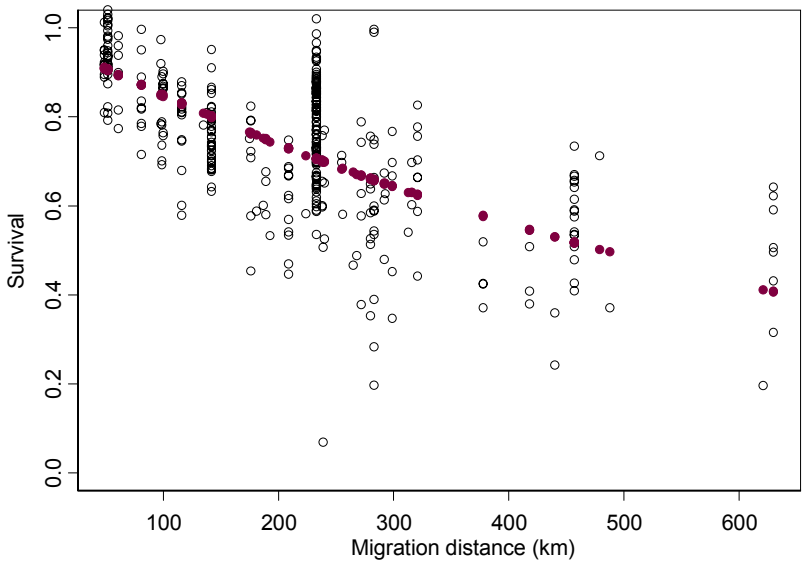

Figure 19. Modeled and observed Snake River spring chinook survival vs. travel distance for migration from hatcheries release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

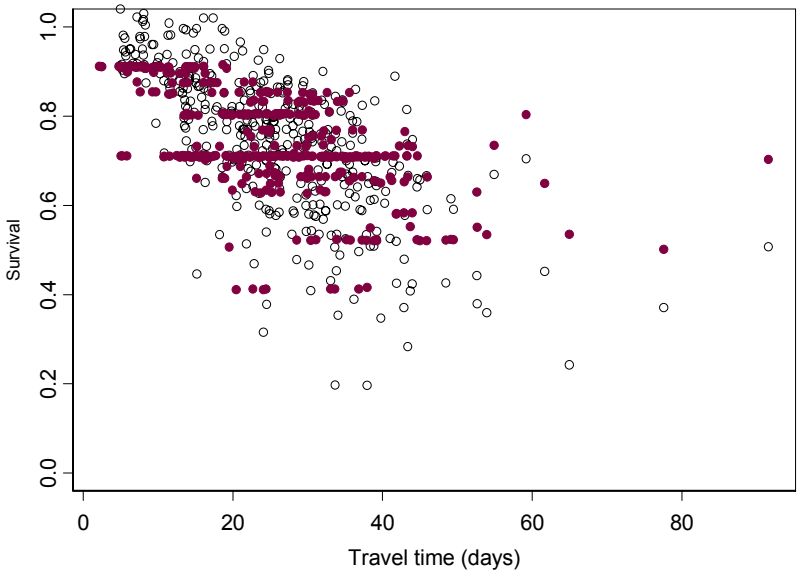

Figure 20. Modeled and observed Snake River spring chinook survival vs. travel time for migration from hatcheries release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

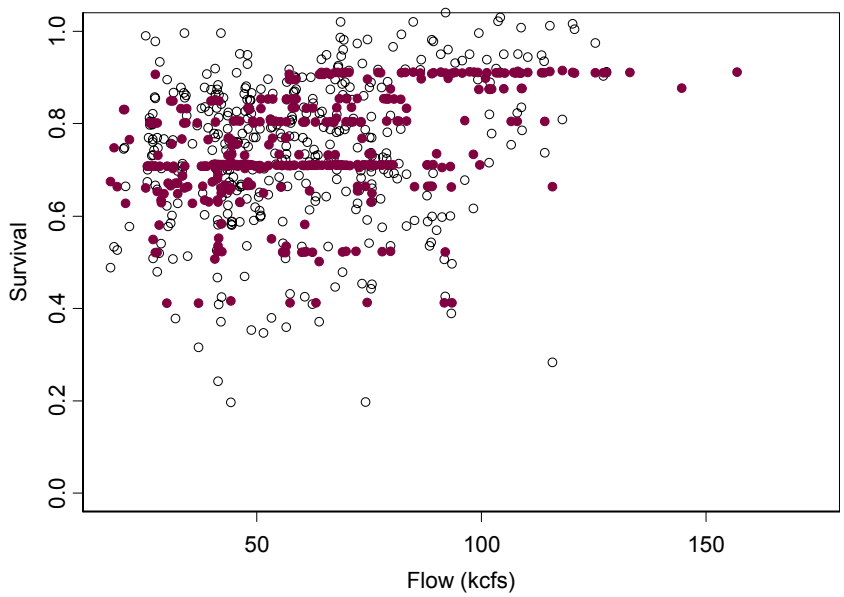

Figure 21. Modeled and observed Snake River spring chinook survival vs. flow for migration from hatcheries release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

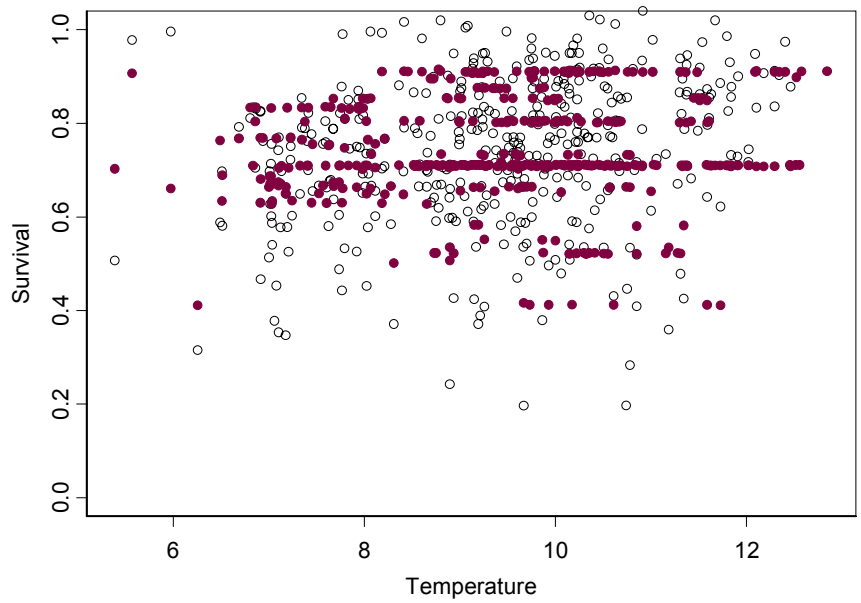

Figure 22. Modeled and observed Snake River spring chinook survival vs. temperature (^{o}C) for migration from hatchery release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the X-model designated (●).

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

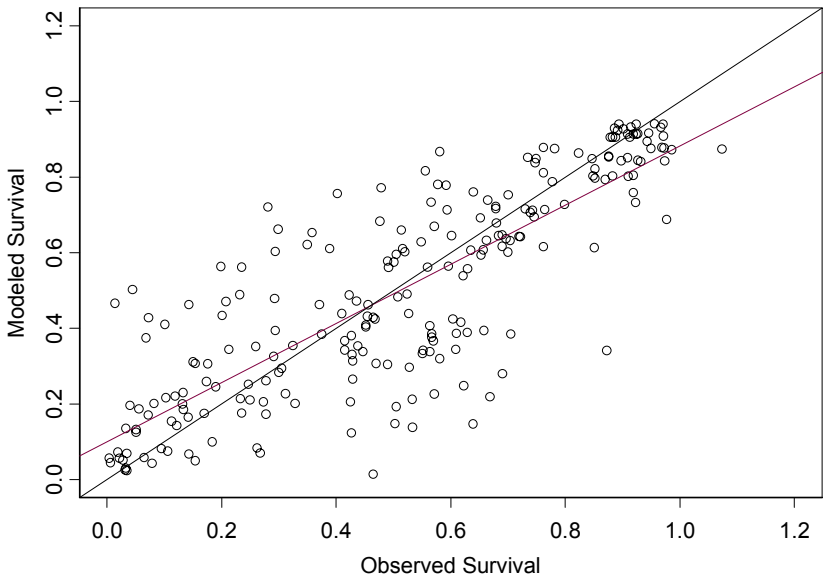

Figure 23. Observed vs. X-model survival for hatchery fall chinook migration between the Snake River release points and LGR Dam over the years 1995-2002 based on 227 data points with no weighting.

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.

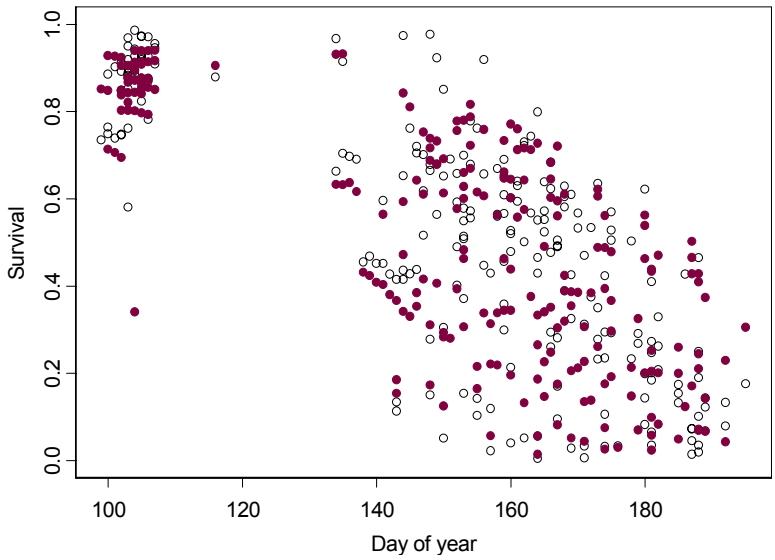

Figure 24. Modeled and observed Snake River fall chinook survival vs. day of the year for migration from Snake River release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

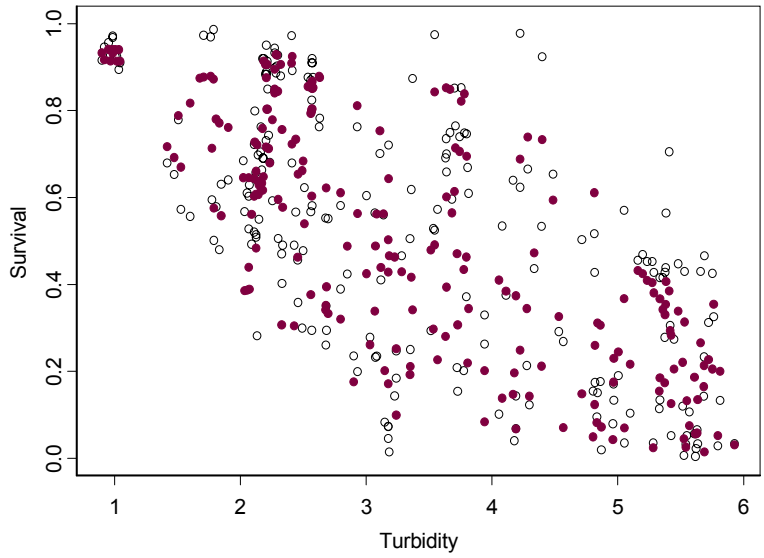

Figure 25. Modeled and observed Snake River fall chinook survival vs. turbidity (ft) for migration from Snake River release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

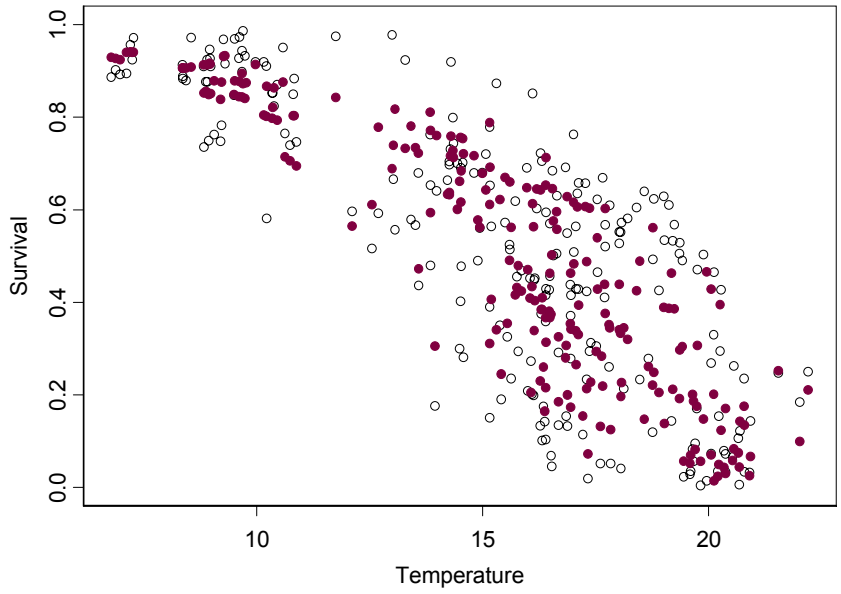

Figure 26. Modeled and observed Snake River fall chinook survival vs. temperature (^{o}C) for migration from Snake River release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

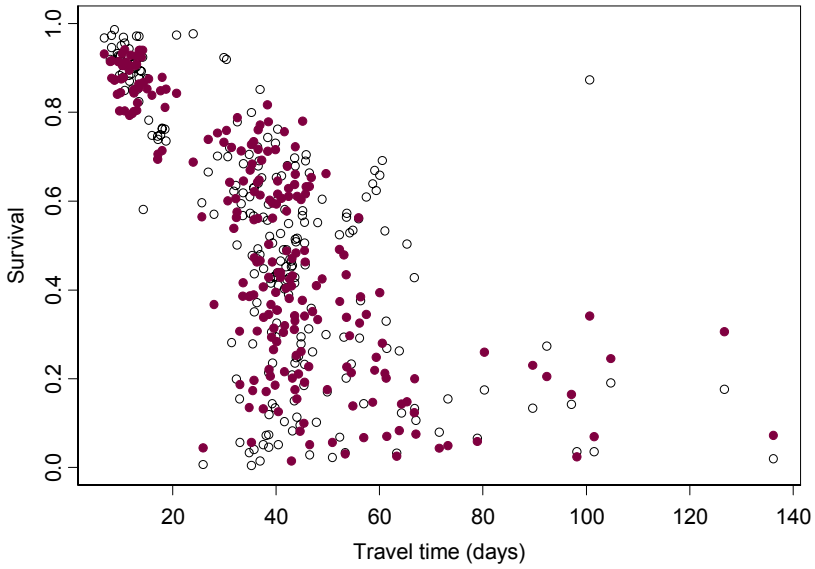

Figure 27. Modeled and observed Snake River fall chinook survival vs. travel time for migration from Snake River release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

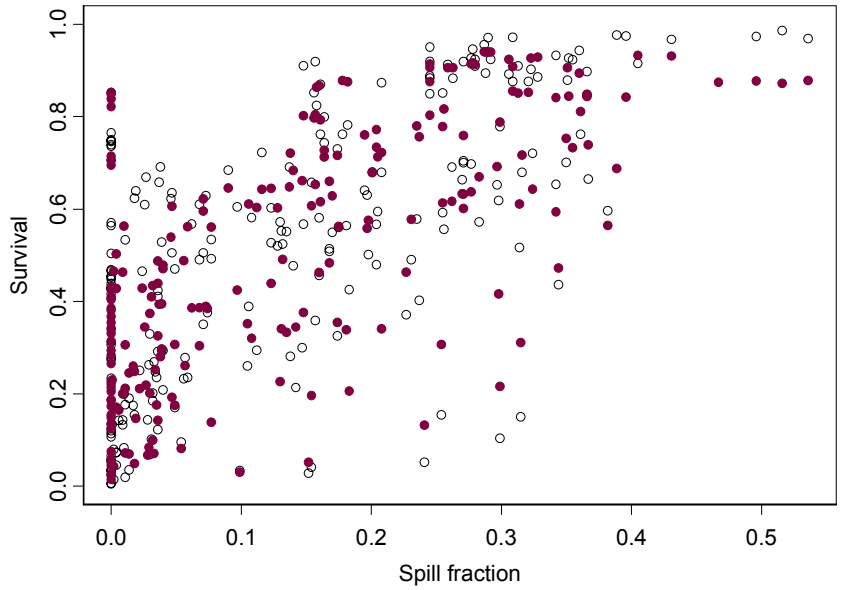

Figure 28. Modeled and observed Snake River fall chinook survival vs. LGR spill fraction for migration from Snake River release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

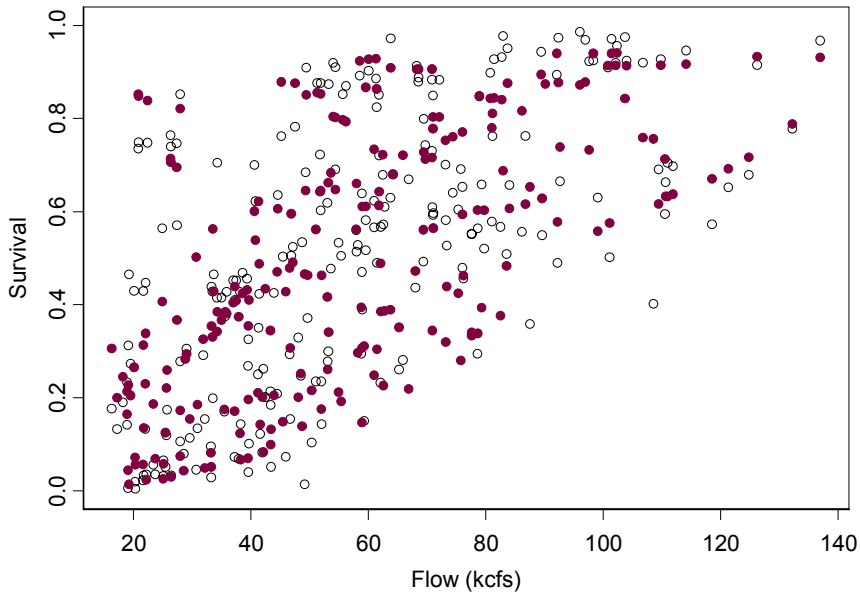

Figure 29. Modeled and observed Snake River fall chinook survival vs. flow for migration from Snake River release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

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.

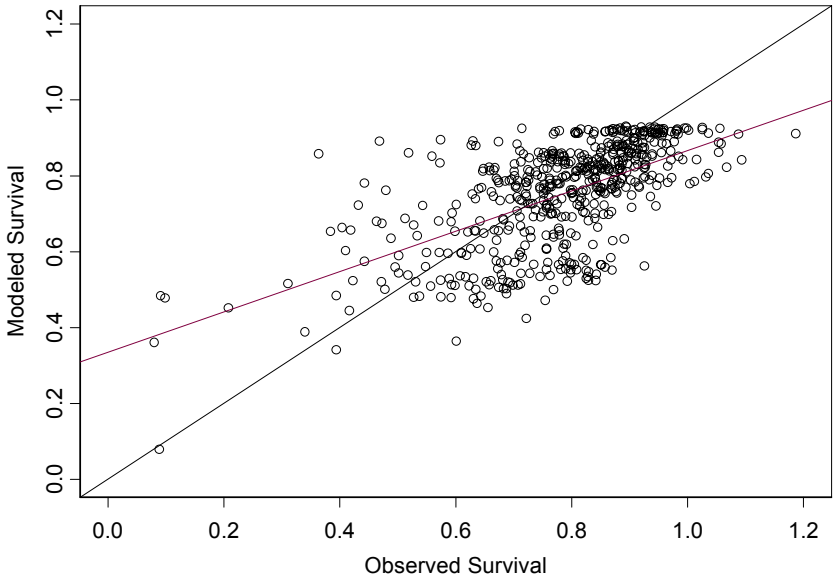

Figure 30. Observed vs. X-model survival for hatchery steelhead migration between the hatchery release points and LGR Dam over the years 1995-2002 based on 555 data points with no weighting.

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.

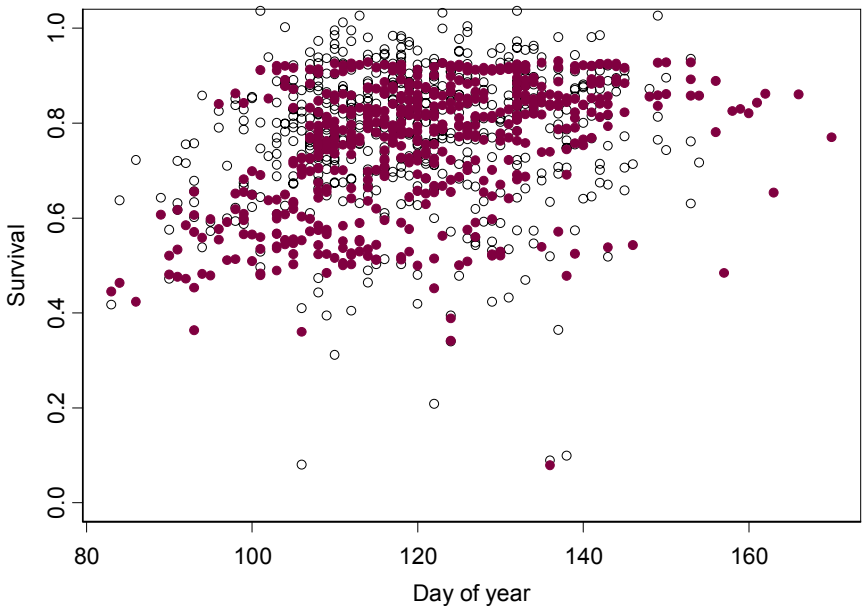

Figure 31. Modeled and observed Snake River steelhead survival vs. day of year for migration from Snake River hatchery release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

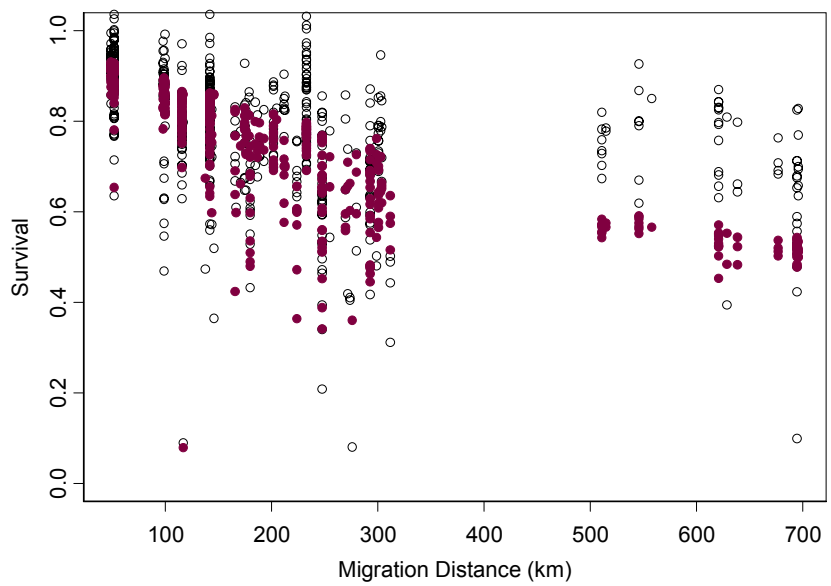

Figure 32. Modeled and observed Snake River steelhead survival vs. migration distance for migration from Snake River hatchery release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

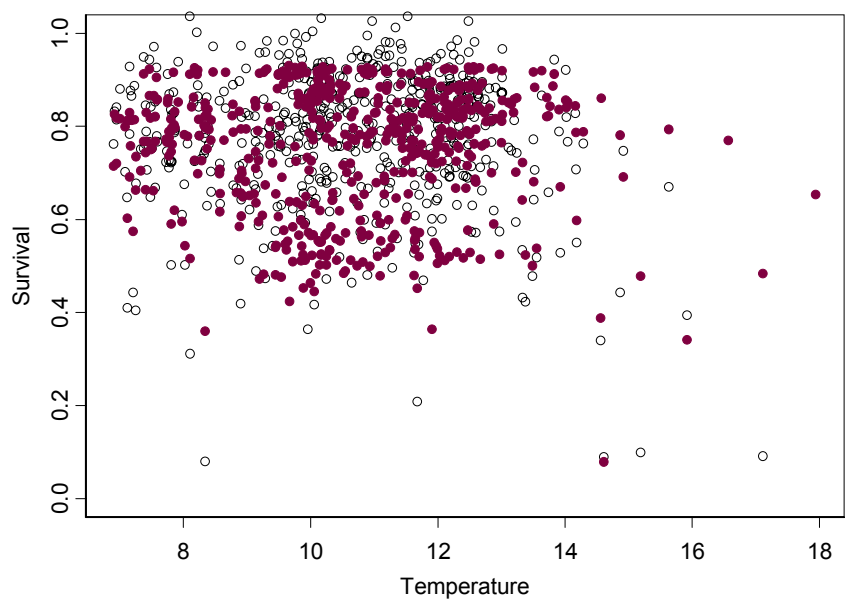

Figure 33. Modeled and observed Snake River steelhead survival vs. temperature (^{o}C) for migration from Snake River hatchery release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

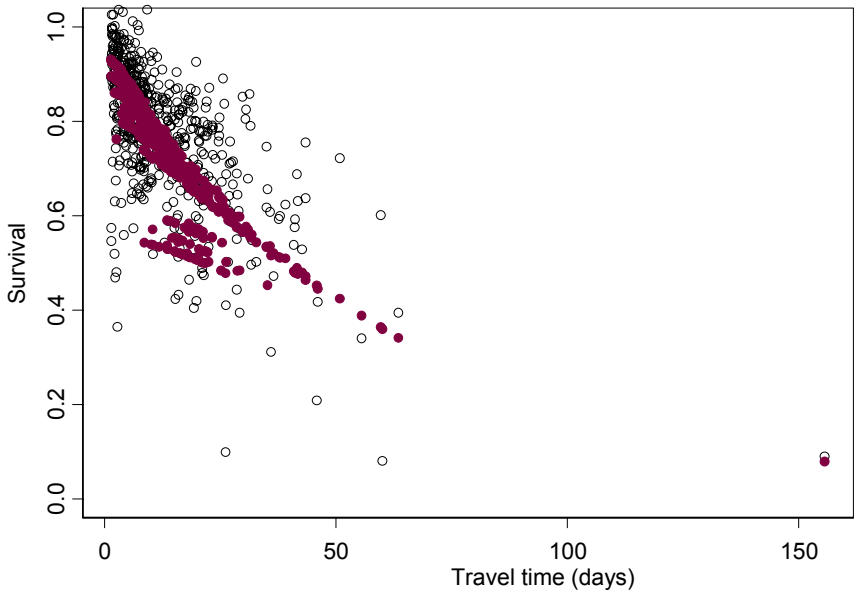

Figure 34. Modeled and observed Snake River steelhead survival vs. travel time for migration from Snake River hatchery release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

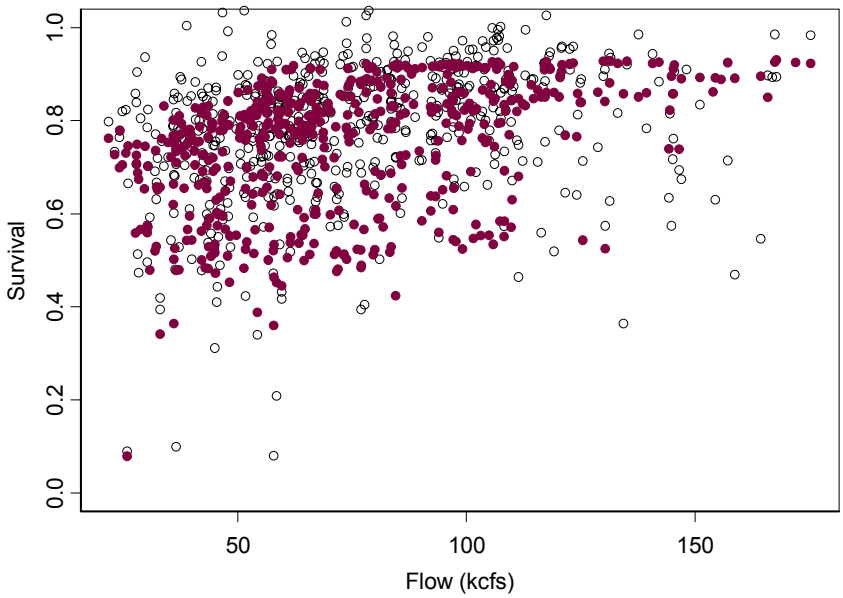

Figure 35. Modeled and observed Snake River steelhead survival vs. flow for migration from Snake River hatchery release sites to LGR Dam between 1995 and 2002. Survival estimated with PIT tags designated (○) survival estimated with the XT-model designated (●).

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.

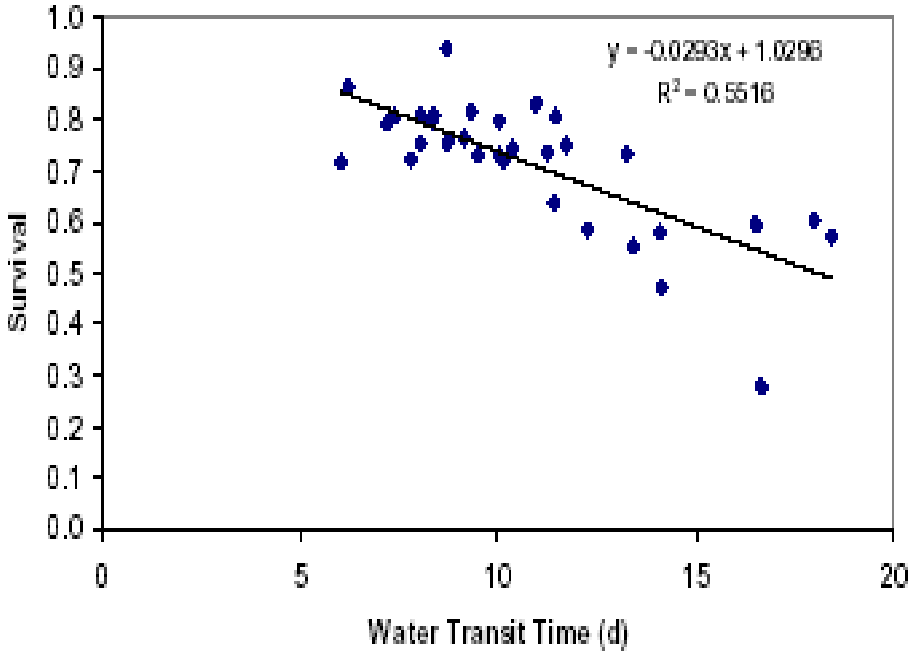

Figure 36. Hatchery spring chinook survival vs. water transit time from LGR to MCN 1998 to 2002 (SFTAFM 2003).

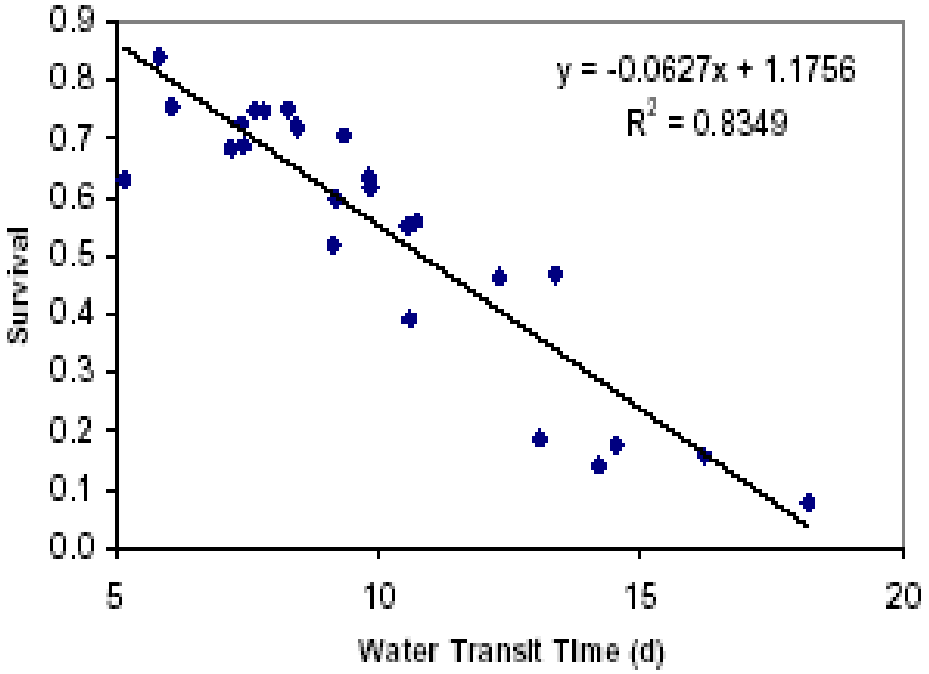

Figure 37. Hatchery steelhead survival vs. water transit time from LGR to MCN 1998 to 2002 (SFTAFM 2003).

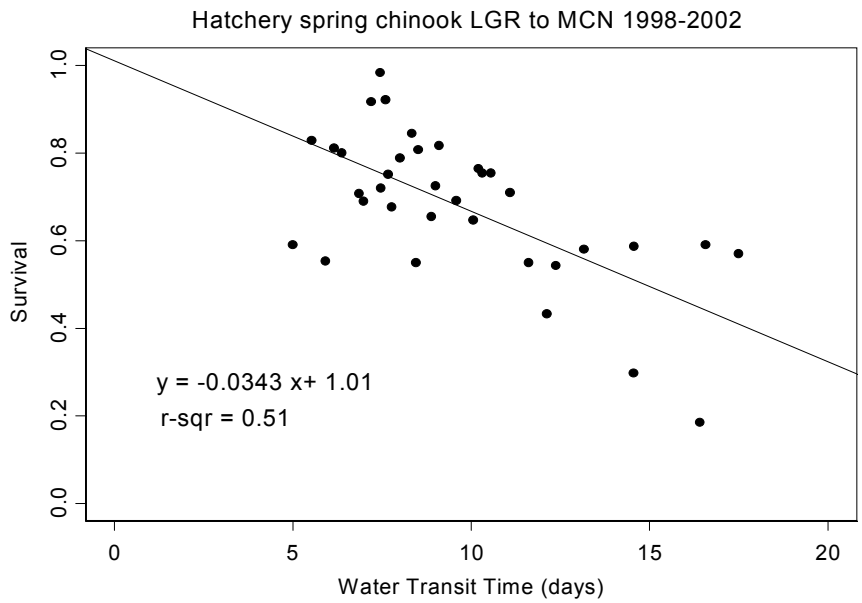

Figure 38. Hatchery spring chinook survival vs. water transit time from LGR to MCN 1998 to 2002 from the data in this report grouped by week of release.

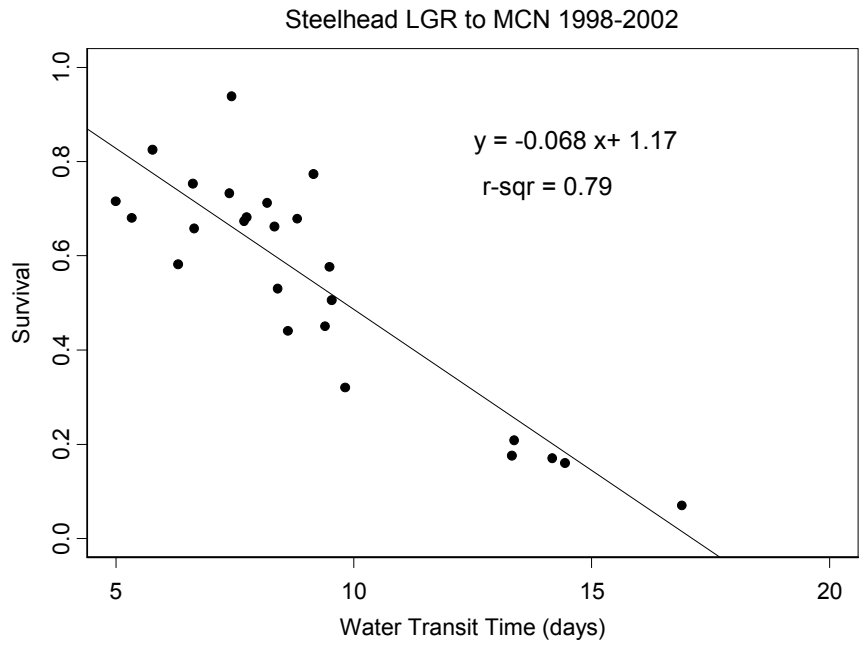

Figure 39. Hatchery steelhead survival vs. water transit time from LGR to MCN 1998 to 2002 from the data in this report grouped by week of release.

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.

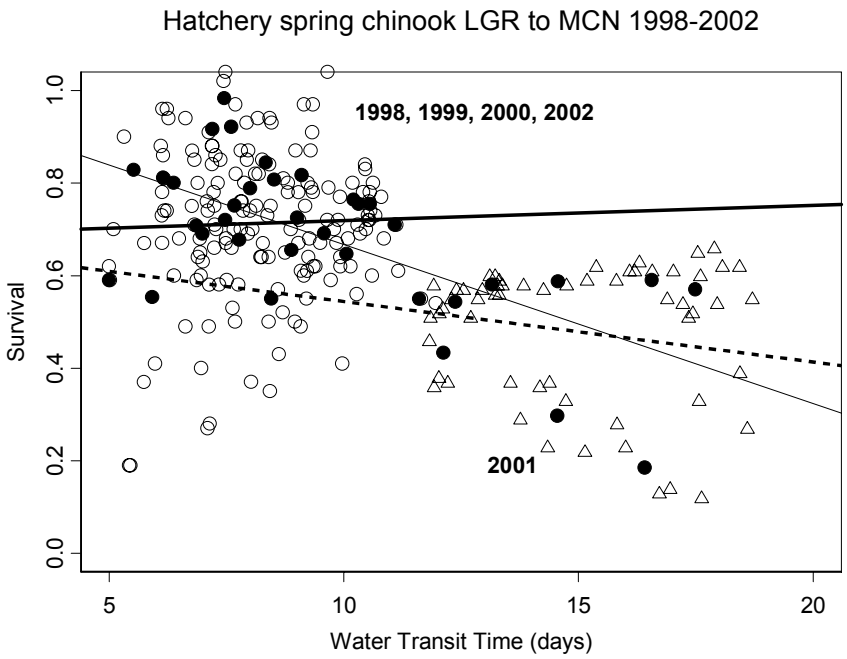

Figure 40. Hatchery spring chinook survival vs. water transit time from LGR to MCN 1998 to 2002 from the data in this report. Daily survivals vs. water transit time for the years 1998, 1999, 2000, and 2002 are designated by (○). For this data, the survival vs. water transit time has no significant slope. 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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