January 29, 2004

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Re: Remand of 2000 Biological Opinion; Review and Comment on NOAA Technical Memoranda; Flow-Survival Relationships

Dear Dr. Stein:

In response to the December 22, 2003 request from Dr. Usha Varanasi, the Idaho Water Users Association and Committee of Nine ("Idaho Water Users") respectfully submit comments on drafts of technical memoranda released by the National Oceanic and Atmospheric Administration (NOAA). Because these memoranda are intended to provide information for revising the 2000 biological opinion (2000 BiOp) on the Federal Columbia River Power System (FCRPS), it is critical that the best available science be included in these documents. As discussed below, the Idaho Water Users find that there are several serious flaws and omissions in the drafts that must be corrected before the memoranda can be used as a basis for consultation.

The Idaho Water Users Association is a non-profit corporation representing irrigation districts, canal companies, ground water districts, water districts, public water suppliers, municipalities, hydroelectric companies, aquaculture interests, agri-businesses, and professional firms. Our members provide water to approximately 2.5 million acres of irrigated farmland throughout Idaho. They own the right to use water from private irrigation reservoirs and those that were built by the U.S. Bureau of Reclamation, as well as natural flow water rights diverted from Idaho's rivers and streams.

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 pursuant to the 1995 and subsequent biological opinions.

Our comments and information are primarily directed at portions of the draft memorandum entitled "Effects of the Federal Columbia River Power System on Salmon Populations" ("Effects Memo") that are likely to be used as a basis for continued calls for flow augmentation from the Upper Snake River in Idaho ("Upper Snake")[1] to purportedly

[1] For purposes of these comments, the Upper Snake River refers to the Snake River and its tributaries in Idaho above Brownlee Reservoir.

benefit listed species of salmon and steelhead. We focus on the sections of the Effects Memo pertaining to the relationships between survival and flow, temperature, travel time and other independent variables ("flow-survival relationships"). We also provide flow-survival comments on the "Role of the Estuary in the Recovery of Columbia River Basin Salmon and Steelhead: An Evaluation of Limiting Factors" ("Estuary Memo"). These comments have been prepared with the assistance of scientists, biologists, and engineers who have studied the relationship of Upper Snake flows to downstream salmon and steelhead survival for more than a decade.

Submission of these comments regarding flow augmentation from the Upper Snake does not mean that the Idaho Water Users agree with the inclusion of off-site measures as part of a Reasonable and Prudent Alternative for operation of the FCRPS. Regardless of the technical issues involved in the consultation, the Idaho Water Users maintain that there is no legal basis for requiring water from the Upper Snake as off-site mitigation for the FCRPS.

As a final introductory matter, a technical memo on harvest issues is noticeably absent among the documents being prepared by NOAA. Of all potential measures to avoid jeopardy and improve recovery, aggressive harvest control strategies are some of the most cost-effective options, especially with respect to fall chinook. The 2000 BiOp recognizes that there is potential to improve survival of the listed species by further reductions in harvest (p. 9-144). The Idaho Water Users strongly support pursuit of harvest reform through the use of selective fisheries, alternative methods and gear, and increasing harvest in terminal areas (2000 BiOp, pp. 9-145-150). We believe that these alternatives can provide tribal fishing opportunities while still reducing the impact of harvest on listed species. A NOAA technical memo exploring these opportunities is sorely needed.

## Draft Effects Memo

**Overview of Issues**

While there are several improvements in the draft Effects Memo in comparison to the 2000 Flow White Paper (NMFS 2000), including recognition of collinearity[2] between flow and other "independent" variables, and passing mention of the recent work by Dr. Anderson regarding the effect of the temperature, significant issues persist. These issues in the draft Effects Memo are listed below and described in more detail in the following sections:

- A hydrological foundation for the analysis is needed.
- The flow-survival analysis does not consider all available recent science.
- A flow-survival relationship does not exist for Snake River yearling migrants, mooting a relationship of flow and steelhead travel time, if any.

[2] In statistical terms, "collinear" means that the predictor or independent variables (e.g., temperature, turbidity, flow, and time of year) are highly correlated with each other. Thus, any correlation of one of the predictor variables with the dependent variable (survival) is confounded by the other independent variables.

- A flow-survival relationship is unlikely to exist for Snake River subyearling chinook.

**Hydrological Foundation**
The 2000 Flow White Paper contained an initial section on hydrology. Although the Idaho Water Users expressed some concerns over the extent and accuracy of that hydrologic analysis, it provided context for the rest of the paper. In response to comments on the 2000 Flow White Paper, NMFS agreed, "that a better understanding of hydrology would be helpful" (NMFS undated). An improved section on hydrology is noticeably absent from the draft Effects Memo. We strongly urge the Service to include background on hydrology as part of the Effects Memo or as a separate document. Attachment 1 contains hydrologic information on the Snake River in Idaho, which would provide perspective on the downstream flow-survival relationships, including those relationships in the estuary and plume of the Columbia River.

**Consideration of All Available Science**
The Effects Memo relies almost solely on four papers to update the 2000 Flow White Paper with respect to flow-survival relationships—Smith et al. (2002, 2003) and Connor et al. (2003a, 2003b). As cited in the sections that follow, a substantial amount of work on flow-survival has been done by other investigators and must be considered as part of using the best available science for the remanded consultation (16 U.S.C. § 1536(a)(2); 50 C.F.R. § 402.14(g)(8)). Additional papers that should be incorporated into the Effects Memo include (in descending chronological order):

- Anderson 2003a, 2003b, 2003c
- Anderson et al. in review
- Beer and Anderson 2004
- Beer et al. 2003
- ISAB 2003
- Anderson and Zabel 2003
- ISAB 2002
- Giorgi et al. 2002
- Anderson 2001
- IWU 2001
- Anderson et al. 2000
- Anderson 2000
- Dreher et al. 2000

In addition, the National Research Council (NRC) is completing a review of flow-survival issues in the Columbia River Basin. Depending on the timing of the release of the NRC report, the Effects Memo should either incorporate the results or note that additional results are forthcoming.

**The Flow-Survival Relationship For Yearling Migrants**

In addition to relying on the studies by Smith et al. (2002) on a "limited segment" of the Lower Snake, the Effects Memo should also refer to the studies that have reached this same conclusion for other reaches of the river system (e.g., Giorgi et al. 2002[3]).

We are not "surprised" by the lack of relationship between flow and travel time for yearling chinook (Effects Memo, p. 57). We have long suggested that physiological characteristics such as the degree of smoltification are more likely to determine migration speed than flow (IWU 1999 and 2000). We applaud the recognition of this fact by the NMFS biologists (Effects Memo, p. 36). Below, we suggest that the same relationship of time of year to travel time is likely to be true for steelhead smolts.

The Effects Memo contains a good discussion of the importance of cues and timing of the smoltification process for steelhead and other yearling migrants (pp. 55-56). However, in contrast to yearling chinook, the Effects Memo finds that steelhead smolt travel time is related to flow based on Smith et al. (2002) and a comparison of Figures 11 and 12 (pp. 36, 62). Although it is true that the travel time for yearling chinook decreased steadily during the early part of the migration season in 2002 and 2003, while the travel time for steelhead did not, examination of Figure 12 suggests that a steady decrease in travel time for steelhead begins on approximately May 10, regardless of flow exposure. Moreover, after May 10, there is not always a direct relationship between flow and travel time (for example, travel time increased in late May 2002 while flow was increasing). Also, the correlation coefficients between travel time variables and date are stronger than the correlation coefficients between travel time variables and flow (Smith et al. 2002; Table 3). Physiological response to photoperiod or water temperature cues (smoltification) is a more likely explanation of the decrease in travel time as the season progresses than increase in flow.

For yearling migrants, the Effects Memo is somewhat ambiguous but appears to suggest a conclusion that <u>survival of yearling chinook and steelhead is not significantly related to flow</u> (p. 36). If so, <u>we agree</u>.

[3] Giorgi et al. (2002) attributed poor steelhead smolt survival in 2001 to the effect of low flows on reduced migration speed. However, we concur with the analysis in the draft Effects Memo that the low 2001 survival appears to be primarily a result of avian predation and temperature effects (Effects Memo, p. 62).

**The Flow-Survival Relationship For Subyearling (Fall) Chinook**

The Effects Memo reports that the migration rate of fall chinook is related to flow, and that survival is related to flow, temperature, and turbidity (p. 36). The Effects Memo also states that "[b]ecause the environmental variables were highly correlated among themselves, determining the relative importance of individual factors was not possible, but all have plausible biological effects on survival" (Effects Memo, p. 36). These results are derived solely from Smith et al. 2003 and Connor et al. 2003a and 2003b.

We disagree with several aspects of the findings of Smith et al. (2003) and Connor et al. (2003a and 2003b), and thus, with those same aspects of the Effects Memo. The Memo notes in passing that "Anderson (2003) argues that increasing temperature most likely leads toward decreased survival" (p. 36). In fact, Dr. Anderson has clearly demonstrated that fall chinook smolt survival above Lower Granite Dam depends on travel distance, travel time, temperature, and turbidity, not on flow (Anderson 2003a and 2003c). In summary, Dr. Anderson and his co-investigators have found:

- NOAA's approach to support a flow-survival hypothesis uses weekly groupings of fish data and relies on multiple regression and graphical analyses (Anderson 2003c; Smith et al. 2003; draft Effects Memo).
- The approach used by Dr. Anderson and others at the University of Washington's Columbia Basin Research group (CBR) uses daily fish data and is based on ecological theory (Anderson 2003a and 2003c; Anderson et al. in review).
- The CBR analysis, which does not include flow as an independent variable, fits within-year flow variable-survival relationships much better than NOAA's approach (Anderson 2003c).
- Fall chinook smolt survival is related to travel distance, travel time, temperature, and turbidity, not flow (Anderson 2003a and 2003c).
- Above Lower Granite, flow augmentation from Dworshak may benefit fall chinook smolt survival by lowering downstream water temperature; however, flow augmentation from Brownlee may reduce smolt survival by increasing downstream water temperature (Anderson 2003c; Anderson 2000; Anderson et al. 2000). From either source, flow augmentation has no effect on travel distance and little or no effect on turbidity and travel time (Anderson 2002; Anderson 2000; Anderson et al. 2000; BLM 2002).[4]
- If a minimum flow target at Lower Granite is to be established, it should be no greater than 25,000 cfs (Anderson 2003b).

[4] The effect of flow augmentation from Brownlee on turbidity is limited by the sediment trap created by reservoir storage, resulting in relatively clear water being released from the reservoir, especially during the summer, regardless of flow (BLM 2002).

**Smith et al. (2003)**

The following issues limit the utility of the research by Smith et al. 2003 and its use in the Effects Memo, particularly with respect to flow augmentation from the Upper Snake:

- The research design and discussion fail to distinguish between flow augmentation from Dworshak versus Brownlee, thus implying that many of the effects from Dworshak are due in part to Brownlee. The paper does not explain or provide data to support its conclusion that summer flow augmentation from Brownlee could ever decrease water temperature. Also, the practical problems of withdrawing cool water from Brownlee during the summer, which are described by Connor et al. (2003a), are not mentioned.
- The analysis relies on correlations between values, not on ecological mechanisms. Also, the flow management differences between Dworshak and Brownlee (e.g., temperature of summer flow augmentation water) are not factored into the discussion of management implications. As a result, the "year-specific curves" suggested for further research are unlikely to be of value to management decisions.
- The water variables at Lower Granite used in the analysis are not entirely representative of Snake River conditions where the fish were released 100 to 200 km upstream because the variables at the dam are influenced by additional inflows and solar heating. In addition, the variables often change substantially during the 40-day or so period between release and identification at LGR dam.
- This study primarily reflects correlations of fish response and water conditions in Lower Granite, not the Snake River, because information in this study and in Connor et al. (2003b) suggests the fish move quickly out of the free-flowing river and then feed in Lower Granite prior to being captured at the dam.
- The analysis excludes subyearling chinook released prior to June when flow and temperatures are lower. For these early releases of fish, which exhibit high survival, flow and temperature both increase over time. If these releases are included, a different pattern emerges than the one described in Smith et al. (2003), which is for post-May release dates when flows are declining and temperatures are rising. Including the early fish releases in the analysis would likely weaken if not break the flow-survival correlation described by the authors. An analysis by Anderson (2003) included these early fish and was able to show that temperature and turbidity (not flow) are sufficient to explain the pattern of survival from April through July. In addition, the Anderson model has a mechanistic basis involving predator search area and activity.
- Anderson (2003c) discusses the fallacy of a 70,000 cfs target.
- In summary, because the fish spent little time in the Snake River above the Clearwater confluence, and because the analysis is fully empirical and confounded with cross variable correlations, it is inappropriate to base Upper Snake River flow augmentation on this study.

**Connor et al. (2003a)**

The following issues limit the utility of the research by Connor et al. (2003a) and its use in the Effects Memo, particularly with respect to flow augmentation from the Upper Snake:

- Like Smith et al. (2003), the research design and discussion fail to distinguish between flow augmentation from Dworshak versus Brownlee, thus implying that many of the effects from Dworshak are due in part to Brownlee. For example, the temperature exposure index reflects the combined inflows to Lower Granite from the Clearwater and Snake Rivers, including flow augmentation from both Dworshak and Brownlee.
- The U.S. EPA temperature model was not developed to address the impacts of Brownlee flow augmentation on temperature in Lower Granite Dam reservoir because the uppermost model point is at Anatone, which is over 160 km downstream of the Brownlee and Hells Canyon Dam, and below the confluence of the unregulated Salmon River.
- During the summer, water warms in Brownlee and then warms further as it is released and moves downstream through Hells Canyon (Anderson 2000). Brownlee augmentation water is typically warmer than the Dworshak augmentation water by 10$^{o}$C or more during the summer (Anderson 2000; Anderson et al. 2000; Connor et al. 2003a).
- Because Brownlee augmentation water is warmer than the Dworshak augmentation water during the summer, flow augmentation from Brownlee will invariably diminish the strong cooling impact of augmentation from Dworshak on the temperature in Lower Granite and downstream. In other words, Lower Granite temperature decreases with Dworshak augmentation and increases with Brownlee augmentation and is dominated by Dworshak operations. Connor et al. (2003a) does not directly address this issue.
- Connor et al. (2003a) identifies a strong correlation between survival to Lower Granite and flow at Lower Granite but does not focus on the actual location where flow and temperature affect survival. In the second 2003 paper, Connor et al. (2003b) calculate that juvenile fall chinook spend about 10 days on average in the free-flowing Snake River and about 40 days on average in Lower Granite Reservoir, which indicates the flow-temperature-survival relationship is primarily determined in the reservoir, not by conditions in the Snake River upstream from Lower Granite. Thus, Connor et al. (2003a) primarily consider the effect of Dworshak on Lower Granite temperatures.
- The unusually weak correlation between flow and temperature for 1998, 1999 and 2000 appears to be due to Dworshak flow augmentation using cool water. Thus, the reduced collinearity between flow and temperature during these years does not suggest that there is separate flow-survival relationship but rather reinforces a temperature-survival relationship.
- Connor et al. (2003a) suggest mechanisms through which flow would affect fish survival. The mechanisms and the flow-survival relationship involve seasonal changes in various factors including turbidity, temperature, and water velocity (Smith et al. 2003; Anderson 2003c; Connor et al. 2003a). Of these factors, water

velocity is the only variable that is affected by flow augmentation to the same extent as seasonal changes in flow. Turbidity is significantly increased by higher seasonal flows reflecting runoff events that transport sediment into and through tributaries. However, flow augmentation from mainstem reservoirs does not increase turbidity because relatively clear water is released after much of the suspended sediment has already settled out (BLM 2002). Similarly, the flow-temperature relationship is different for seasonal flows in comparison to augmented flows. In the seasonal flow-temperature relationship, temperature and flow increase together up to the peak of the spring runoff; then the relationship reverses and flow decreases while temperature continues to increase. With augmented flows during the summer, temperature decreases with increasing Dworshak augmentation but temperature increases with increasing Brownlee augmentation. The analysis by Connor et al. (2003a) assumes flow augmentation will produce the same effects as seasonal flows. Except for velocity, which is greatly attenuated in the reservoirs, this is unlikely to be true. As Dreher et al. (2000) demonstrate, significant velocity increases in the reservoirs are not achievable using Upper Snake flow augmentation.

- Independent of temperature, the hypothesized biological benefits of increased flow might result from decreased travel time and increased turbidity. However, other studies have produced conflicting results regarding the correlation of travel time and flow for fall chinook (e.g., Smith et al. 2003; Anderson et al. 2000). In any event, no relationship between smolt survival and travel time has been demonstrated. And, as discussed above, there is no evidence that flow augmentation from the Upper Snake significantly increases turbidity.
- The draft Effects Memo fails to include one of the key conclusions of Connor et al. (2003a)— that summer flow augmentation from Brownlee cannot currently deliver cool water to the Snake River for practical reasons.

**Connor et al. (2003b)**

The following issues limit the utility of the research by Connor et al. (2003b) and its use in the Effects Memo, particularly with respect to flow augmentation from the Upper Snake:

- Like Smith et al. (2003), the research design and discussion fail to distinguish between flow augmentation from Dworshak versus Brownlee, thus implying that many of the effects from Dworshak are due in part to Brownlee. For example, the temperature variable reflects the combined inflows to Lower Granite from the Clearwater and Snake Rivers, including flow augmentation from both Dworshak and Brownlee.
- Connor et al. (2003b) correlate flow and temperature at Lower Granite Dam with travel time in the free-flowing Snake River. In the paper, they recognize that there is a weakness in the analysis because Lower Granite conditions were used as surrogates for conditions experienced by the fish in the free-flowing reach. This approach is only valid if there is a consistent relationship between the two locations. In fact, this is not the case. The Lower Granite indices, in addition to being several hundred kilometers downstream of the free-flowing reaches, were

computed over 50+ day intervals although the fish were only in the river reaches for approximately the first 10 days of the interval. These differences make the indices poor surrogates of the conditions experienced by the fish in the river. Also, the 50-day average Lower Granite temperature and the 10-day average Snake temperature at Anatone can differ by up to 7ºC as a result of cooler inflow from the Clearwater River, including Dworshak flow augmentation (data from CRDART, http://www.cqs.washington.edu/dart/dart.html). As a result, the Connor et al. (2003b) conclusions regarding the factors that affect migration rate through the free-flowing reach of the Snake River are not supported.

- It appears that one of the reasons for a relatively high correlation in the travel time models is that distance traveled is on both sides of the regression equation in all three models.
- Because of the strong correlation between flow and temperature, it is not clear that the flow-travel time model is really independent of the temperature-travel time model.
- The hypothesis that increased flow operates to reduce travel time by increasing velocities is highly questionable, at least with respect to any sort of management implication such as flow augmentation. Within reservoirs, a substantial increase in flow velocity would require enormous quantities of flow augmentation (Dreher et al. 2000). Above Lower Granite, if the fish really travel faster due to higher velocities, it is not clear that this would result in biological benefits because the smolts would just be moved down to Lower Granite faster to continue rearing.

**Effects Memo Conclusions/Summary**

The lack of a summary of conclusions in the draft Effects Memo makes it impossible to fully comment on the document. The Idaho Water Users may submit additional comments once this section is drafted.

## Draft Estuary Memo

**Overview of Issues**

NMFS concludes that changes in flow amount and timing would improve habitat in the estuary and provide survival benefits to juvenile salmonids migrating through the estuary or the Columbia River plume (Estuary Memo, pp. 29, 52-54). The issues of concern to Idaho Water Users in the draft Estuary Memo are listed below and described in more detail in the following sections:

- The discharge from the Snake River at Lewiston, which includes the Upper Snake, is similar in timing and quantity for the past 93 years. Also, there is minimal potential to augment Columbia River flows using Upper Snake water.
- Flow augmentation from the Upper Snake would have an inconsequential effect on environmental conditions in the main stem and smolt arrival time in the estuary.

**Hydrology**

As illustrated in Figure 4 of Attachment 1, the volume and pattern of flow in the Snake River upstream from Lower Granite Reservoir has not changed significantly over the past

93 years. Thus, any habitat degradation that may have occurred in the Columbia River estuary or plume due to alteration of flow quantity or timing is not the result of development of the Upper Snake. Further, the flows required to make significant improvements of habitat in the estuary or plume are so large that any attempt to use Snake River augmentation water for that purpose will be just as futile as trying to restore pre-development water velocity through the hydropower system using Snake River flow augmentation. Snake River flow is a small portion of the total flow of the Columbia River at the estuary and the natural variation in flows between years dwarfs the contribution of the Snake River, let alone the much smaller volume of Snake River flow augmentation.

Figure 4 of Attachment 1 illustrates the consistency in discharge timing and quantity of the Snake River at Lewiston between the pre 1948 period and post 1983.[5] Unlike the discharge of the Columbia River at the estuary, the present May-July discharge is 86% of the pre 1948 period. As discussed in Attachment 1, much of the reduction in peak discharge is the result of flood control operations as evidenced by the increased discharge from flood control releases in January through March. Figure 5 of Attachment 1 is provided for comparison of the variation in discharge that occurs between years as compared to the variation in discharge that has occurred over time. The variation between the discharge in 1995, 1996 and 2002, none of which were record years, is clearly greater than the average variation between the pre 1948 and post 1983 periods in Figure 4.

Table 1 illustrates that the flow of the Columbia River at the beginning of the estuary is at least 10 times greater than the flow of the Snake River at Weiser under both high and low flow conditions. It is impossible to try to restore the lower Columbia to pre-development conditions using augmentation from a source that provides less than 10 percent of the flow during the spring and summer.

Table 1 also compares minimum and maximum monthly discharges of the Columbia River at Beaver Army Terminal near Quincy, Oregon with the monthly discharge of the Snake River at Weiser during the same month. The Beaver Army Terminal gage is located at river mile 53.8 within the area of the river affected by tidal flow. Even though the gage record is relatively short—16 years of records, some partial, from 1968 through 2003—it serves to show the wide variation in annual flow of the Columbia River. The variation in monthly flow from high (1997) to low (2001) years (20.5 MAF in May and 21.5 MAF in June) is more than the average annual flow of the Snake River at Weiser (13.1 MAF) for the period of record.

[5] The pre 1948 period represents conditions prior to the construction of the Hells Canyon Complex, Dworshak Dam, and many of the Reclamation reservoirs in the Upper Snake. The post 1983 period represents current conditions after all of the storage had been constructed.

**Table 1. Minimum and maximum monthly discharge of the Columbia River compared to Upper Snake River discharge in that month.**

| Month | Minimum Flow (MAF) | | | Maximum Flow (MAF) | | |
|---|---|---|---|---|---|---|
| | Year | Lower Columbia River | Upper Snake River | Year | Lower Columbia River | Upper Snake River |
| April | 2001 | 9.0 | 0.6 | 1969 | 24.2 | 2.3 |
| May | 2001 | 10.7 | 0.6 | 1997 | 31.2 | 2.5 |
| June | 2001 | 9.1 | 0.5 | 1997 | 30.6 | 2.9 |
| July | 2001 | 6.1 | 0.4 | 1997 | 17.2 | 1.1 |
| August | 2001 | 6.5 | 0.4 | 1999 | 13.7 | 0.8 |

Another way to consider the futility of using flow augmentation from the Upper Snake River to significantly improve flows in the estuary or plume is to compare the period of record average flow of the Columbia River at Beaver Army Terminal for July, a relatively low flow month during the period of flow objectives, to recent levels of Upper Snake River flow augmentation. The average monthly flow of the Columbia River for July at this location is 13.0 MAF for the period of record at the Beaver Army Terminal gage. If the entire 427,000 acre-feet of Upper Snake River flow augmentation were released in July, it would be only 3 percent of the average monthly July flow of the Columbia River at Beaver Army Terminal. Figure 6 in Attachment 1 shows Upper Snake River flow augmentation from 1995-2003 in relation to the flow of the Columbia River at the mouth and further illustrates the futility of using Upper Snake flow augmentation for changes to the estuary.

Idaho Water Users believe that augmenting flows in order to significantly change the estuary or plume would be fruitless and an ineffective use of water resources.

**Environmental Effect of Upper Snake Flow Augmentation on the Estuary and the Plume**

The Estuary Memo finds that flow reductions and changes in the Columbia River estuary have adversely affected habitat availability, spatial structure, and diversity in the estuary and ocean plume (Estuary Memo, pp. 29, 52-54). The implication of these findings is that increased flows would provide habitat benefits in the estuary and plume. Also, increased flow is implied to offset some of the adverse impacts from dredging, diking and other human activities in the estuary (Id., pp.28, 32-36, 52-54). In summary, the Estuary Memo concludes that "water flow has a likely medium to high impact on recovery potential for salmon populations, high for salmon life histories that utilize shallow water associated habitats, and medium to low for salmon expressing life history strategies that utilize deeper associated habitats" (Id.).

As described in the previous section of these comments, there has not been a reduction or timing change of flow from the Upper Snake to the Columbia River. Thus, adverse effects on habitat in the estuary and plume did not result from storage and diversions of water in the Upper Snake. Similarly, augmentation from the Upper Snake can only

provide a de minimis contribution to the flow in the Columbia River estuary and plume and thus little or no benefit to habitat in those locations.

Given the unaltered flows from the Upper Snake, the minimal potential to augment Columbia River flows using Upper Snake water, and the lack of biological benefits from such augmentation, there is no reason to consider flow augmentation from the Upper Snake to benefit salmon in the Columbia River estuary or plume.

Thank you for consideration of these comments. Please contact us if you have any questions.

Sincerely,

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## ATTACHMENT 1

## HYDROLOGY OF THE SNAKE RIVER IN IDAHO

### Overview

The total annual outflow from Idaho into the Columbia River system is about 70 million acre feet (MAF), or roughly one-third of the total flow of the Columbia River (IWRB 1996). About one-half of this flow is provided by northern Idaho tributaries and one-half is from the Snake River. Average annual flow of the Snake River as it leaves the state at Lewiston is about 36 MAF (Id.). Roughly one-third of this amount comes from the Upper Snake River above Hells Canyon and about one-half comes from the Salmon and Clearwater River basins (Id.). The remainder is contributed from smaller tributaries in Oregon, Washington, and Idaho.

Records of stream flow and irrigated acreage do not extend back to the beginning of irrigation in the mid-1800s, but data are available since 1910. Changes to stream flow caused by the construction of reservoirs and development of irrigation on about 1.5 million acres should be reflected in the flow records for the Snake River at the Weiser gage, located just above Brownlee Reservoir. However, the historical record does not reflect a significant decrease in flow. Conversely, average annual flows have remained constant since 1910, as discussed in the following section.

### Historical Stream Flow Records

Figure 1 shows the observed mean annual flow of the Snake River at Weiser for the period 1911-2003. As can be seen from the trend line plotted on the chart, average annual flows have <u>remained constant</u> over the past 93 years despite water development in the Upper Snake River basin.[1]

Figure 2 contains the same mean annual flow data used to prepare Figure 1 and also shows the development of irrigated acreage in Idaho and the development of Upper

[1] The large variation in mean annual flow of the Snake River at Weiser in recent years causes the slope of the least squares trend line to fluctuate slightly above and below zero. For example, the severe drought in 2001 has caused the trend line to change from slightly positive to slightly negative. A least squares trend line can be over sensitive to extreme values near the beginning or end of a record; therefore, this fluctuation is not unexpected and does not reflect a long-term trend of increasing or decreasing flow.

Snake Bureau of Reclamation (Reclamation or BOR) water storage.[2] Figure 2 shows that irrigated acreage significantly increased and most of the Reclamation storage development occurred after flow measurement records for the Snake River at Weiser began. Figure 2 also shows both irrigated acreage and Reclamation storage increasing throughout the period but without a significant change in the mean annual flow of the Snake River at Weiser.

Figure 3 shows the observed mean annual flow of the Snake River as it leaves the state at Lewiston. The flow is now considered Lower Granite inflow because the backwater of the reservoir extends upstream beyond the state line. As can be seen from the trend line plotted on the chart, average annual flows have remained constant here over the past 93 years as they have at Weiser. Even though most of the irrigation development in Idaho has occurred upstream from Weiser, both the Idaho Power Hells Canyon complex and Dworshak Dam are downstream of Weiser and any impact from those developments would only be apparent by examining the flow of the Snake River as it leaves the state as shown in Figure 3.

Figures 1 through 3 show the average mean annual discharge of the Snake River has not changed for the past 93 years. Fisheries biologists have expressed concern that even if the mean annual discharge is the same, the shape of the hydrograph may have changed

[2] Reclamation storage (BOR storage) represents all reservoirs above Brownlee. The irrigated acreage is taken from Census Reports and includes all irrigated acres in Idaho (United States Census Office, 1902-1997). Census Reports do not separate the number of irrigated acres by river basin within a state. The irrigated acreage reported for Idaho includes acreage outside of the Snake River basin upstream from Weiser including the Bear and Salmon River drainages. Similarly, the reported irrigated acreage does not include acres irrigated from the Snake River basin above Weiser that are located in Wyoming, Nevada, and Oregon. The differences in the chart from actual acreage irrigated from the Snake River basin upstream from Weiser is minimal because most of the irrigated acreage in Idaho is irrigated from the Snake River basin upstream from Weiser and most of the acreage irrigated from the Snake River basin above Weiser is in Idaho.

significantly. Figure 4 shows a comparison of the Lower Granite[3] inflow (discharge of the Snake River at Lewiston) hydrograph for the periods pre 1948 and post 1983. The pre 1948 period is divided into the periods 1916 to 1922 and 1929 to 1947 only because mean daily discharge data is not available for the period 1923 to 1928. The pre 1948 period ends prior to influences from the Hells Canyon Complex, Dworshak Dam, and many of the Upper Snake Reclamation reservoirs. The period 1984 to 2003 was chosen to be representative of current conditions and to match the average mean annual volume of the pre 1948 period after flow augmentation releases were removed from the current period. That is, the average mean annual discharge of the pre 1948 period is the same as the average mean annual discharge of the post 1983 period after the releases for flow augmentation were removed from the post 1983 average annual discharge.

Matching the average mean annual discharge for this comparison is appropriate because, as Figure 3 demonstrates, there has not been a long-term change in the mean annual discharge for the 93-year period from 1911 to 2003.

Figure 4 shows the shapes of the hydrographs for the two periods pre 1948 and post 1983 to be similar with the peak discharge in the recent period occurring at about the same time as the earlier period. Not surprisingly, the peak discharge is somewhat smaller due to flood control operations and filling reservoirs in the drainage. The winter discharge is higher in the recent period due to flood control releases made in response to snow surveys and runoff forecasts. Likewise, the late summer discharge is higher, even with flow augmentation removed, as a result of irrigation return flows.

The difference in the hydrographs in Figure 4, comparing discharge pre 1948 and post 1983, are much more consistent than hydrographs of individual years as shown in Figure 5. Figure 5 compares hydrographs for 1995, 1996, and 2002. 1995 is a year of average mean annual discharge; 1996 is an above average but not record runoff year; and 2002 is a below average but not a record dry year. The difference between the hydrographs in

[3] The Lower Granite inflow location was chosen for this analysis of seasonal changes because the Snake River discharge at Weiser hydrograph may be modified by the Hells Canyon complex prior to the discharge entering the reach inhabited by anadromous salmonids and steelhead.

Figure 5 is clearly more than the variation between the early and late period hydrographs in Figure 4. This comparison demonstrates the average seasonal discharge of the Snake River at Lewiston (Lower Granite inflow) is more consistent between predevelopment and current conditions than the variation in discharge between individual years.

## The Columbia River Estuary

As noted above, the entire discharge from the State of Idaho to the Columbia River basin is about one-third of the discharge of the Columbia River at the estuary. The discharge of the Snake River at Lewiston is about one-sixth of the discharge of the Columbia River at the estuary and, as discussed above, is substantially unchanged over the past 93 years. Finally, the discharge of the Snake River at Weiser is about one-sixteenth of the discharge of the Columbia River at the estuary.

Figure 6 compares the discharge of the Columbia River at the Beaver Army Terminal at river mile 53.8 to the discharge of the Snake River below Hells Canyon Dam for the period 1995 through 2003. Figure 6 also shows the flow augmentation component of the Hells Canyon discharge for each year. The flow augmentation in Figure 6 is the combined flow augmentation form the Upper Snake (the Snake River above Brownlee Reservoir) and the augmentation from Brownlee Reservoir provided by Idaho Power Company. It is irrational to speculate that meaningful modifications to the discharge of the Columbia River at the estuary can be achieved by manipulating flows from a source whose entire discharge is less than the monthly fluctuations of the Columbia River.

## Summary

In summary, the quantity and timing of Snake River flow has not changed significantly from at least 1911 to the present. In 1995, the National Research Council recognized this fact:

> *"Because there has not been a major shift in the Snake River hydrograph, it is doubtful a priori that the declines in Snake River salmon stocks are due to or reversible by changes in the seasonality of the flow regime of the Snake River alone"* (NRC 1995 at 193).

Likewise, the National Marine Fisheries Service recognized in their 2000 White Paper "Salmonid Travel Time and Survival Related to Flow in the Columbia River Basin" on page 1:

> *"Accordingly, storage regulation changes are less pronounced in the lower Snake River than in the Columbia River."*

The lack of change to the historical flows of the Snake River in Idaho has been shown repeatedly. The operation of the Snake River is different than the operation of the Columbia River and that difference needs to be recognized in the analysis of management alternatives.

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**Figure 1.**
**Snake River @ Weiser**
**Mean Annual Flow**

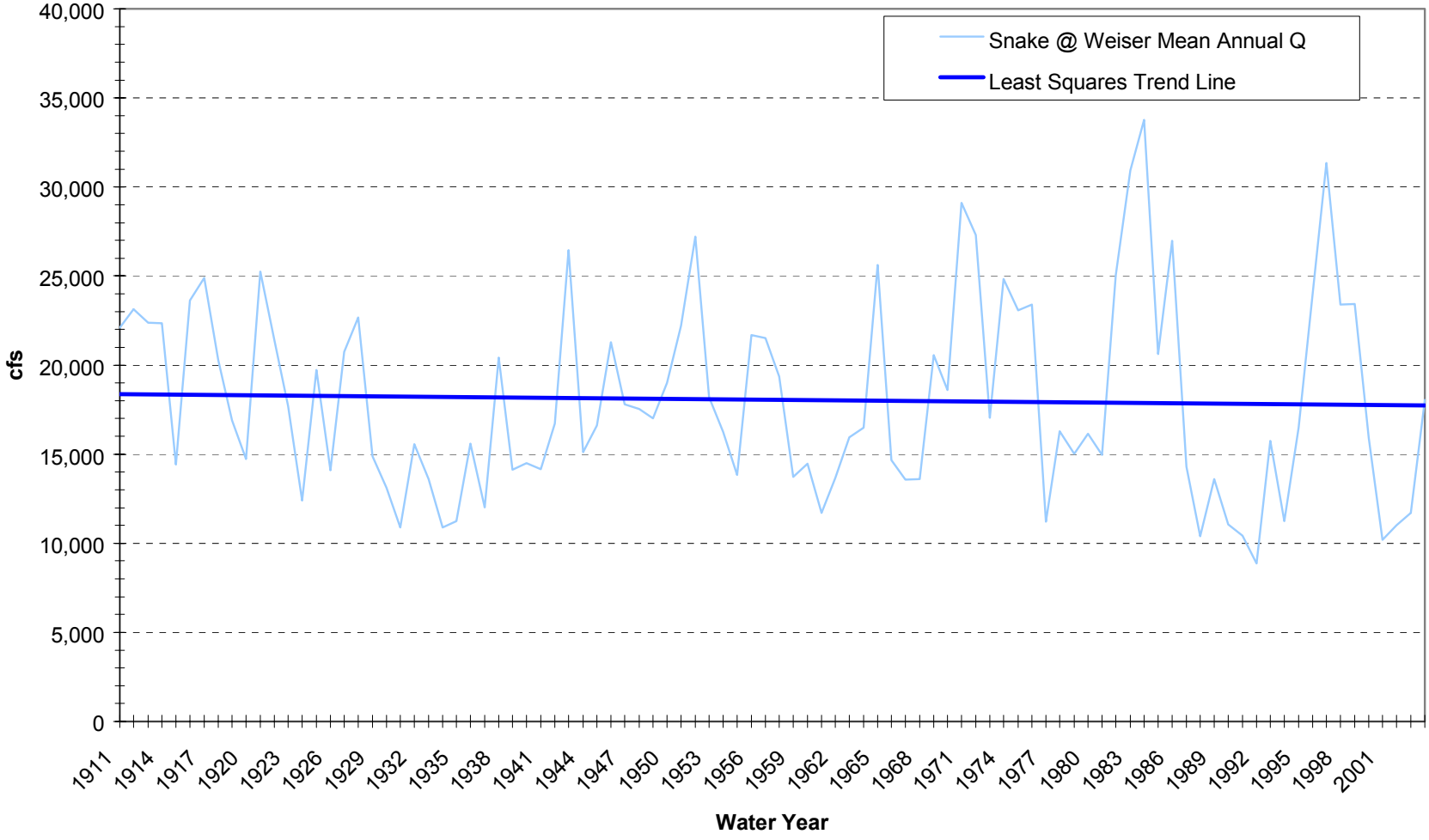


**Figure 2.**
**Snake River @ Weiser Mean Annual Flow, Irrigated Acres, and Reclamation Storage**

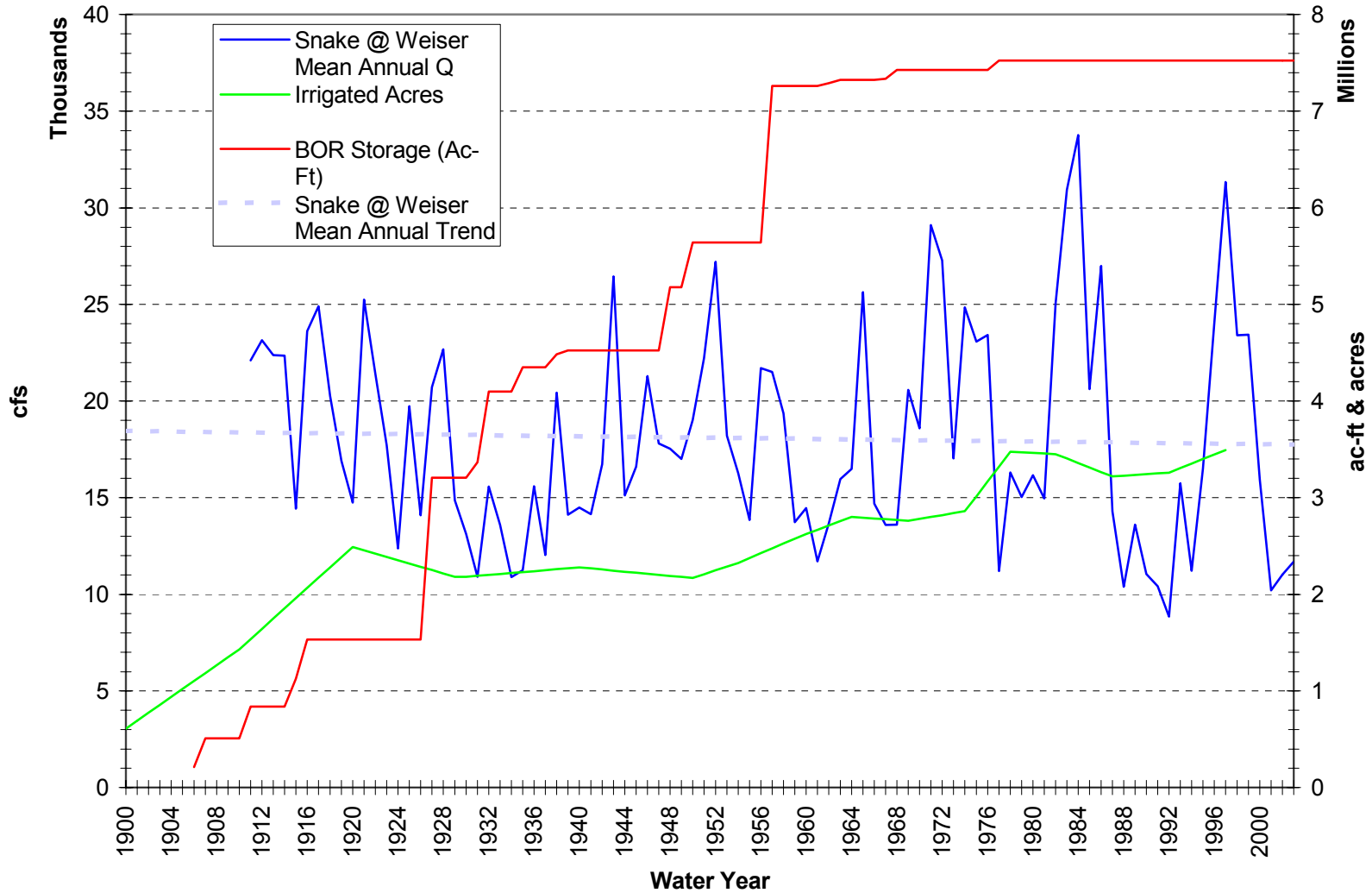


**Figure 3.**
**Lower Granite**
**Mean Annual Inflow**

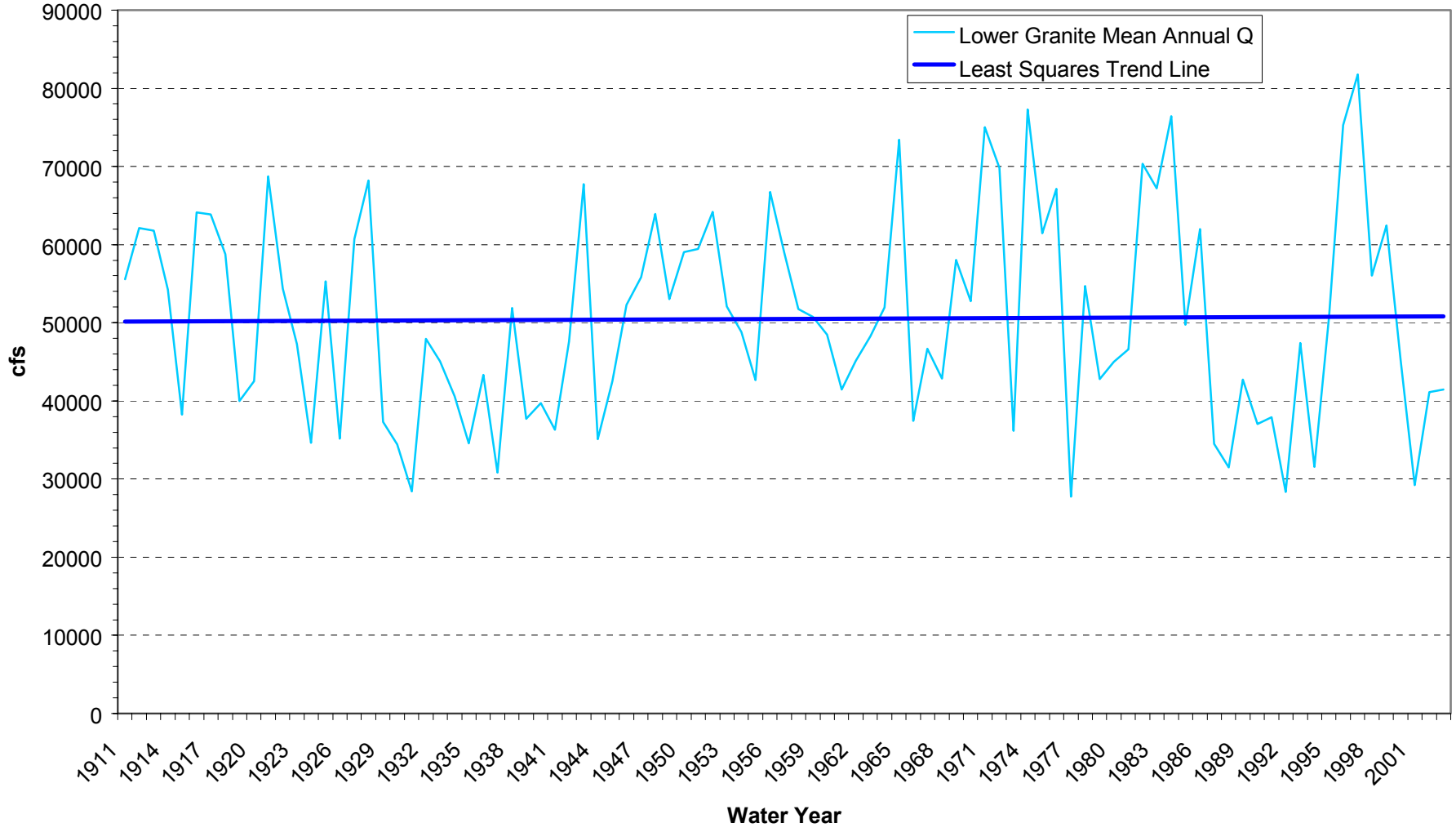


**Figure 4.**
**Lower Granite Mean Daily Inflows for Periods Shown**

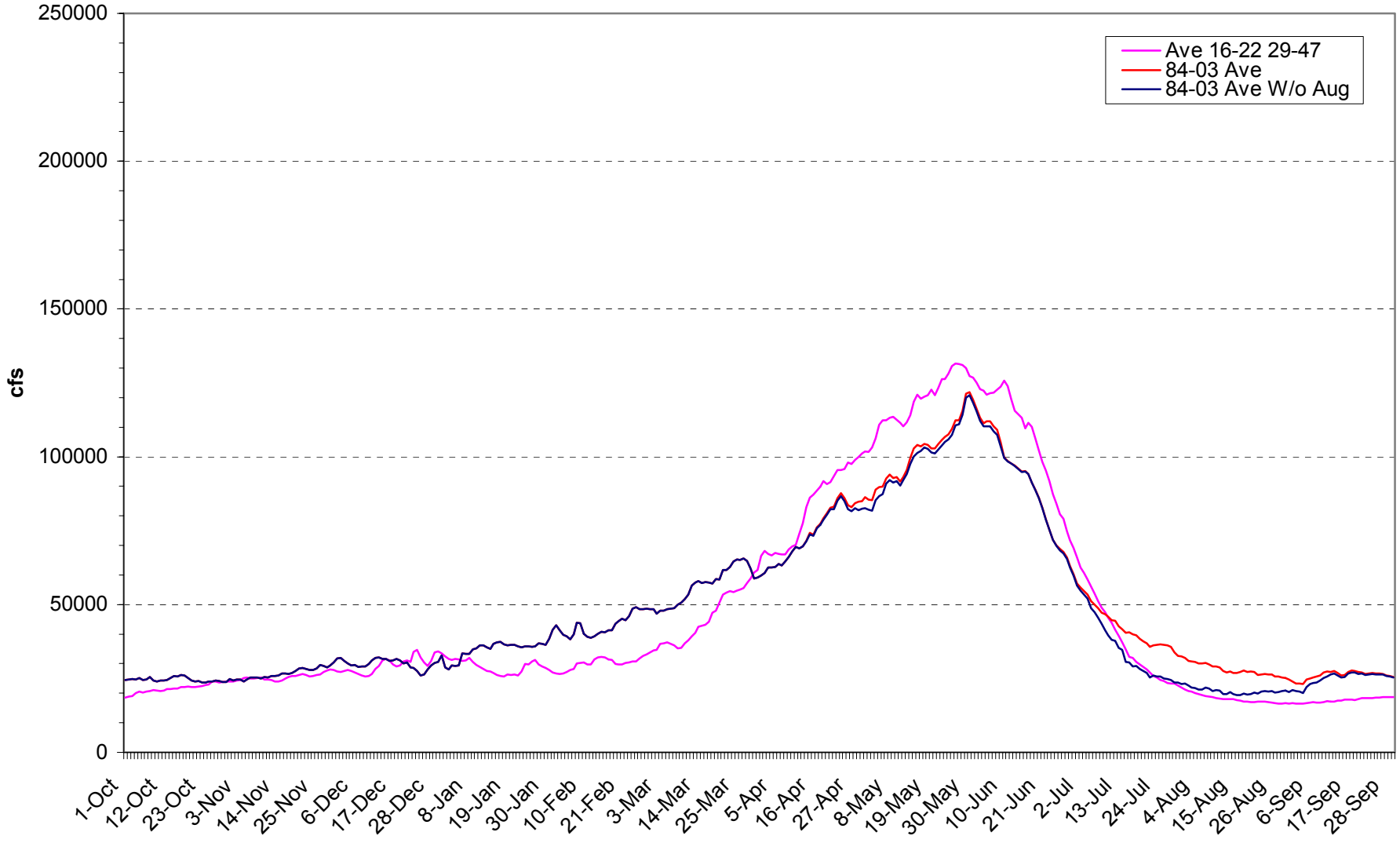


**Figure 5.**
**Lower Granite Mean Daily Inflows for 1995, 1996, and 2002**

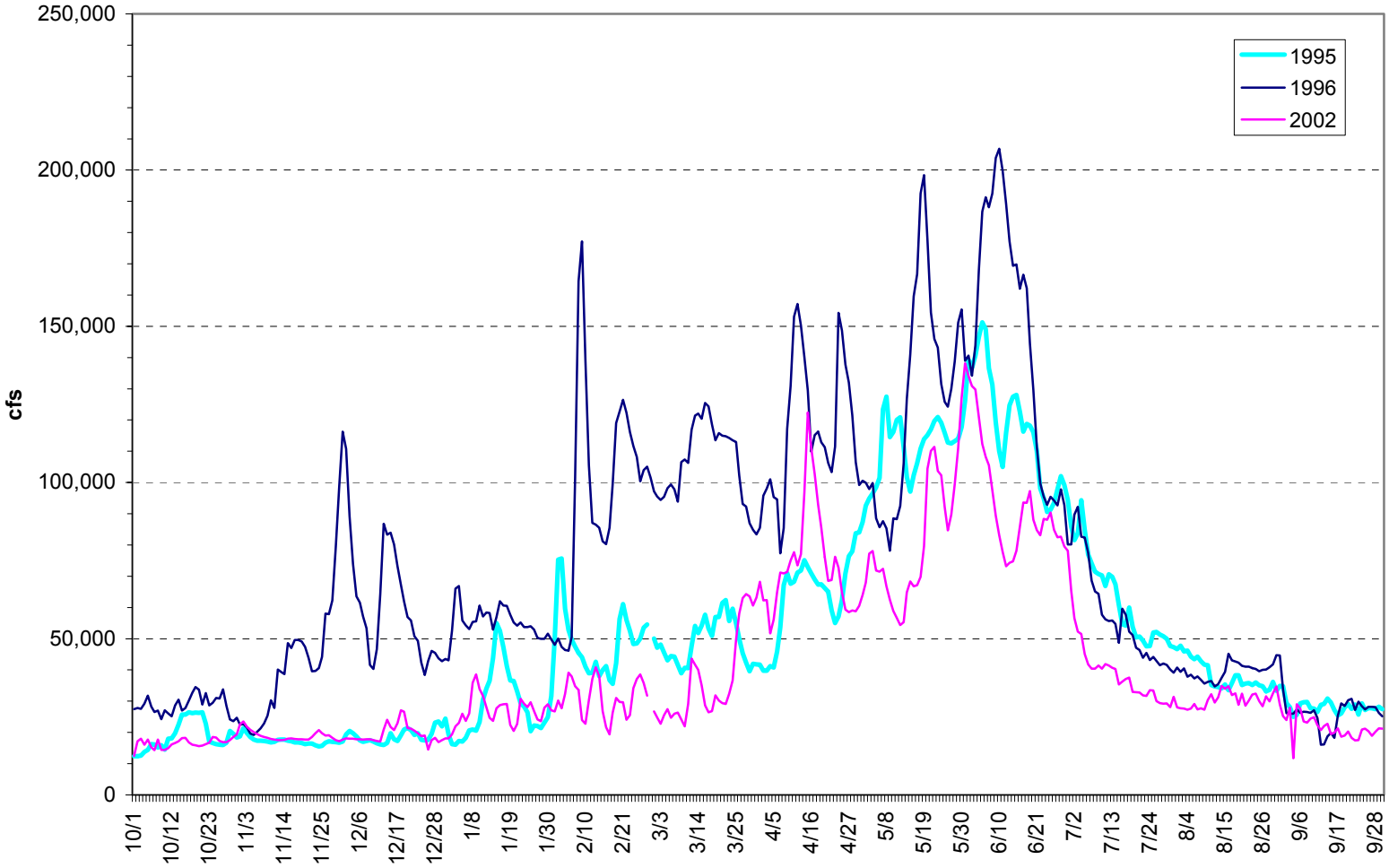
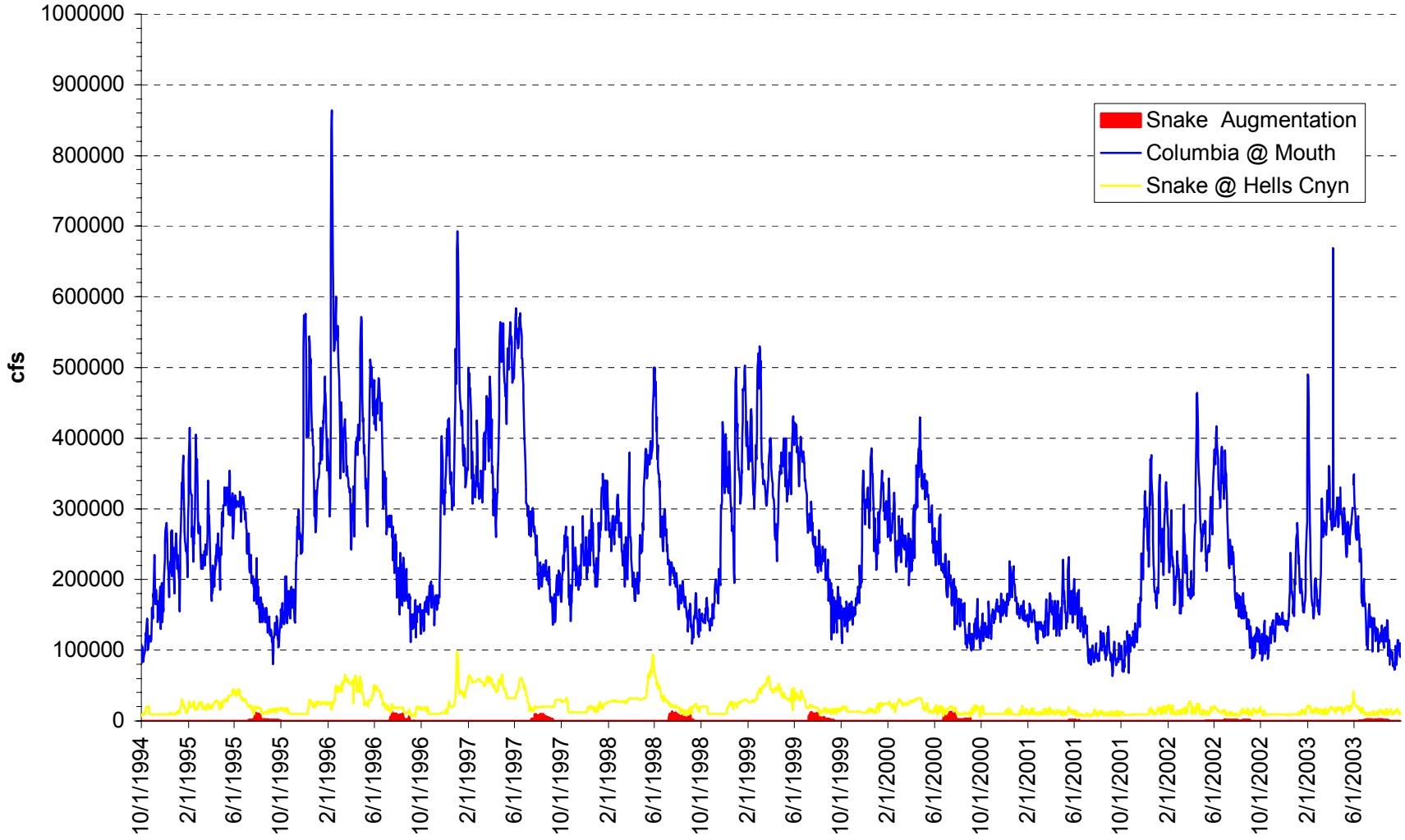


**Figure 6.**
**Snake River Flow Augmentation Compared to the Columbia River near the Mouth And the Snake River at Hells Canyon -- 1995 - 2003**



# Attachment 2

# Toward a Resolution of the Flow/Survival Debate and the Impacts of Flow Augmentation and Water Withdrawal in the Columbia/Snake River System

# Toward a Resolution of the Flow/Survival Debate and the Impacts of Flow Augmentation and Water Withdrawal in the Columbia/Snake River System

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December 4, 2003

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## Introduction

The National Marine Fisheries Service (NMFS) 2000 Biological Opinion for the operation of the Federal Columbia River Power system defined adequate water quality, quantity, and velocity as essential features of the critical habitat of the juvenile salmon migratory corridor. To meet these features NMFS established a series of Reasonable and Prudent Actions (Actions 14-39) related to water management. Of particular significance RPA 14 calls for seasonal flow targets at Snake and Columbia River dams and RPA 27 restricts water depletions in the basin until the recovery is achieved (NMFS 2000). These RPAs are based on a controversial "flow/survival" hypothesis, established more than two decades ago, which states that more flow would benefit juvenile salmon during their migration, with more flow being provided by augmentation from reservoir releases or fewer water withdrawals (Anderson 2001). In 2003, hypotheses on the factors affecting smolt survival have undergone significant revision and review. These include updates of the data and new analyses by National Oceanographic and Atmospheric Administration (NOAA) (Williams et al. 2002), the Columbia Basin Fish and Wildlife Authority (CBFWA) (FPC 2003; Petrosky et al. 2003), and Columbia Basin Research of the University of Washington (CBR) (Anderson 2003a, b). In addition, reviews were conducted for the Northwest Power and Conservation Council (NPCC) (Giorgi et al. 2002; ISAB 2002), and a review requested by Washington State is being conducted by the National Research Council (NRC). Although these new analyses and reviews examine essentially the same information, they treat the information differently, and reach conclusions that are similar in some aspects but radically different in terms of the effect of flow changes on smolt survival. This white paper discusses these analyses and

demonstrates that the information now exists to resolve the issue of the impacts of flow augmentation and water withdrawals on smolt survival.

## Hypotheses on factors affecting in–river survival

The analyses and reviews of the impact of flow alteration on smolt survival conducted to date can be divided into three independent hypotheses, developed by CBFWA, NOAA and CBR. All three analyses include new PIT tag observations and correlate estimated smolt survivals with water quality properties. The analyses use different data groupings; the CBFWA and NOAA estimate survival through the Snake and Columbia hydrosystem for data blocked by the week of arrival at Lower Granite Dam. The CBR analysis blocks data by the daily arrival at the dam. All analyses estimate the average environment experienced by the fish for the respective data blocks. While the analyses used somewhat different selections of the data and grouped them differently (Table 1) these differences are not significant to the conclusions reached in the analyses.

**Table 1. Comparisons of survival analysis approaches.**

| Analysis Group | Data Treatment | | | Survival Covariates | | | | | | Type of Analysis |
|---|---|---|---|---|---|---|---|---|---|---|
| | Years | River Reach | Block Size | Spill[1] | Flow[2] | FTT[3] | WTT[4] | Tem[5] | Tu[6] | |
| CBFWA | 1998-2001 | LGR-IHR | week | ● | | | ● | ● | | MLR[7] model on yearly data |
| NOAA | 1995-2001 | LGR-MCN | week | | ● | | | | | Graphical analysis on yearly data |
| CBR | 1995-2002 | LGR-MCN | day | ● | | ● | | ● | ● | ET[8] model on seasonal and yearly data |

1) Proportion of river spilled experienced by fish during migration. 2) Average flow experienced by fish over migration. 3) Fish travel time. 4) Water travel time. 5) Average temperature experienced by fish over migration. 6) Average turbidity experienced by fish over migration. 7) Multiple liner regression model. 8) Ecological theory model. LGR = Lower Granite Dam, IHR = Ice Harbor Dam, MCN = McNary Dam.

Major differences can be seen among the approaches. CBFWA combines data over all years in multiple linear regressions and demonstrates in-river smolt survival correlated with the proportion of water spilled, water travel time (WTT) (a calculated surrogate for flow), and water temperature. CBFWA demonstrates that survival could be linearly related to WTT for data combined over years (Figure 1). CBFWA does not present analyses for survival within years, claiming that within-season relationships would not appear because juvenile survival is the result of many direct and indirect environmental and biotic variables, described as averages over a period of time, and although variations within a year exist, the in-season variations are not sufficient to characterize it (Petrosky et al 2003).

NOAA (Williams et al. 2002) analyzes smolt survival between LGR and MCN for the years 1995 through 2001. The survival data are blocked into weekly groups and graphically correlated with an index representative of the flow experienced by the fish during the migration. Combining data for all years, the authors suggest that the flow/survival pattern could be described by a hockey stick curve with a linear flow-dependent part at low flows and a flow-independent part at high flows. The threshold for the break in the curve is about 100 kcfs (Figure 2).

The CBR analysis is derived from ecological theory for the survival of smolts through dams, how smolts interact with their predators, and how temperature, exposure time, and turbidity affect predator/prey interactions (Anderson 2003a; Anderson et al. in review). The significance of each variable was determined by fitting the model to survival data of the passage of chinook and steelhead data migrating through the Snake/Columbia river system. The spill proportion and distance traveled were the most important variables. The coefficient describing the effects of travel time was small indicating that travel time contributed generally less than 5% to the reservoir survival through the hydrosystem (Anderson 2003a). Neither fish travel time nor travel velocity, both of which correlated with flow, were important factors in determining the change in survival within years or between years.

The CBR model is fit to data grouped between years and within years. That is, the model is fit to data for all years combined and to data from each year to explore the seasonal variations in survival within each year. Both the between-year and within-year data sets were fit well by the model; temperature is a major variable accounting for differences in survival between years and within each year (Figure 3). However, because of the within-year and between-year flow and temperature relationships (Figure 4), the observed flow and survival relationships are also fit by the model for between-year (Figure 5) and within-year data (Figure 6).

The three analyses all exhibit relationships between flow measures and survival for data grouped between years (Table 2). The CBFWA analysis produces a linear regression between survival and WTT, and the NOAA and CBR analyses produce hockey stick relationships between survival and flow. So, using data grouped between years, it might be concluded that smolt survival relates to flow directly or to some attribute related to flow. However, this hypothesis must be rejected when looking at the within-year data. The CBFWA analysis specifically states that the survival-WTT relationship was not evident within a year. The NOAA in an earlier analysis demonstrated no consistent flow/survival relationships for spring chinook and steelhead (Smith et al. 2002). In contrast, the CBR analysis, which does not include flow, fit well for within-year flow/survival patterns. The inability of flow-based explanations to reproduce the within-year patterns is strikingly illustrated by plotting the NOAA flow-based hockey stick model and the CBR temperature-based model against the within-year flow/survival relationship for spring chinook in 2001 (Figure 6). In fact, no explanation based on flow is able to fit the observed within-season survival patterns because flow exhibits a seasonal peak while survival generally declines over the season.

**Table 2. Comparison of model fits to data between years.**

| Analysis Group | Spring chinook | | Steelhead | |
|---|---|---|---|---|
| | N | r-square | N | r-square |
| CBFWA | 66 | 0.65 | 26 | 0.87 |
| CBR | 1015 | 0.71 | 315 | 0.82 |

Although survival through the Snake River and McNary Dam can be correlated with flow using between-year data blocks, a relationship is not evident for 163 groups of PIT tagged fall chinook smolts migrating through John Day Reservoir between June 21 and August 8 over the years 1999-2002 (Figure 7). Individual and combined year regressions of flow against survival showed no statistically significant relationship with p-values ranging between 0.69 to 0.345 and r-squares from 0.018 to 0.075. The survival vs. flow slopes of the regressions ranged between -0.002 to 0.0019 for individual years and was 0.0004 for the combined year data.

In addition to considering how well the flow and temperature based models fit or do not fit data, their theoretical bases also need to be considered. The NOAA model has no theoretical basis, and is simply two straight lines fit by eye through a cloud of data. The CBFWA model has no theoretical basis either, although there is a reference to the success of the transition to seawater depending on physiological condition changes over time, and arrival at estuary within the "biological window" (Petrosky et al. 2003). However, this reference to the transition to seawater does not address how survival in the hydrosystem is related to water travel time. Only the CBR model has a basis in ecological mechanisms: the probability of encounters between resident predators and migratory smolts (Anderson et al. in review) and the effect of temperature on predator and prey activities (Anderson 2003a). In essence, in the model smolts pass through a gauntlet of stationary predators; their mortality depends on the number of predators encountered, which depends on migration distance, and temperature, which affects predator metabolic activity.

## Delayed mortality effects

Although we can soundly reject the flow alteration/survival relationship as a factor in fish survival through the hydrosystem, how river flow and especially flow augmentation may affect the survival of fish in the estuary and ocean must still be considered. Researchers have demonstrated that the condition of the juvenile fish during their freshwater life stage is correlated with their return rate as adults (Beckman et al. 1999; Ward and Slaney 1988) and have hypothesized that the timing of ocean entry affects adult survival (Budy et al. 2002). This link between freshwater experience and ocean survival is sometimes referred to as "delayed mortality"; although the issue is complex, we can estimate the relative importance of flows on delayed mortality. In particular, we can estimate the effect of flow augmentation and water withdrawals on delayed mortality to within an order of

magnitude. To do this, we consider how these flow actions incrementally affect fish travel time and water temperature, two factors that may relate to delayed mortality.

Fish travel time, while not affecting survival in the hydrosystem, does affect the estuary arrival time and the total duration of exposure of the migrating fish to the river environment. Increased water temperature, besides affecting migration survival directly, can also increase the fishes' metabolic demand during migration. Together these factors could decrease the condition of the fish entering the ocean and so increase their mortality rate. The fractional change in delayed mortality from flow augmentation and water withdrawals will be approximately proportional to the incremental change in river temperature and travel time from the actions. The CRiSP smolt passage model (CBR 2003), which has been calibrated with 15 years of PIT tag data, quantifies the effect of flow alteration on travel time. For example the model predicts that each change in flow by 1000 cfs measured at Lower Granite Dam changes the spring chinook travel between the Salmon River and Bonneville Dam by 2 hours. Therefore, water withdrawals that decrease flow by 1000 cfs would increase a 26 day travel time to 26 days and two hours. A one million acre feet flow augmentation from Dworshak Reservoir over a 40-day period would decrease the travel time from 26 to 25 days. Thus, water withdrawals should have unmeasurable and insignificant impacts on fish travel time and major flow augmentations should decrease travel time by less than 5%. Therefore, the effect of these actions on delayed mortality through a change in migration time is small to insignificant.

The impact of these flow altering actions on delayed mortality through temperature can be made in a similar manner. First, flow augmentation may increase or decrease the water temperature. Flow augmentation from the Dworshak Reservoir decreases river temperature through the upper dams of the lower Snake River. However, because river temperatures closely follow air temperatures (Mohseni et al. 1998) the temperature impact deceases with distance from the source of augmentation as the water equilibrates with the air temperature. The impact is greatest for fish traveling between Dworshak and Lower Granite Dam (Connor et al. 2003), but the effect of Dworshak water downstream is greatly reduced, and the impact on fish survival through the hydrosystem is very small (Beer and Anderson 2003). Furthermore, flow augmentation from the Brownlee Reservoir on the upper Snake River can increase downstream river temperature (Anderson 2000), and thus would have a small negative impact on smolt survival (Anderson et al. 2000). Thus, over a two week migration period, the total degree days of exposure of fish with flow augmentation in the Snake River is essentially the same as the exposure without augmentation.

The impact of water withdrawals on river temperature may also be positive or negative, depending on whether the temperature of the withdrawal's return flow is higher or lower than the river temperature. Returns from surface runoff or municipal waste water may be warmer than the river water while subsurface returns may be cooler. However, whatever the effect, the magnitude of change in the river temperature is proportional to the amount of water withdrawn relative to the river flow. A 1 kcfs return flow that is $1^{o}C$ warmer than a 100 kcfs river flow would increase the river temperature by $0.01^{o}C$. We are fairly safe in concluding that the impacts of water withdrawals of this magnitude have an

insignificant and unmeasurable impact on river temperature and therefore on delayed mortality or direct in-river survival.

# Exploring larger impacts

Although we can reasonably conclude that incremental flow augmentation and withdrawals on the order of a several kcfs have unmeasurable impacts on in-river survival and delayed mortality, we need to consider whether larger flow alterations outside the ranges considered here may have some catastrophic impact on the ecosystem and fish survival. Although such projections are speculative, we can evaluate the potential problems by addressing some of the ecological pathways through which the environment affects salmon. In particular, we can explore whether increased impacts proportionally degrade the ecosystem or if there are critical thresholds at which the system degrades. Below we address critical thresholds related to flow and temperature.

## The flow threshold

Intuitively, when flow is reduced to zero, hydrosystem survival is zero. The NOAA between-year analysis (Williams et al. 2002) demonstrated a hockey stick pattern where survival became dependent on flow at a threshold of 100 kcfs. The CBR analysis showed that this break was generated by temperature, not flow. Furthermore, an analysis presented to the IASB indicates that the flow/survival threshold is much lower than the one postulated by NOAA (Anderson 2003b). Data shows that Dworshak hatchery spring chinook survival to Lower Granite Dam between 1990 and 2001 was independent of flow over a range 34 to 133 kcfs (Figure 8). The CBR model fits this data well and indicates that the flow/survival break point is on the order of 25 kcfs and is very sharp. Furthermore, the model provides a mechanism for the break point. When the fishes' migration velocity, which is determined by flow, drops below the random velocity between the predator and fish, survival no longer depends on the distance through the predator gauntlet. Because the fish movement is predominantly random below the threshold, the number of predators encountered depends on the migration time. Therefore, below the flow threshold, flow affects survival through its effects on migration time. Thus, both evidence and theory suggest that flow only affects fish survival below the lowest flow ever observed in the Columbia/Snake River system. The ISAB hypothesis that variable water velocities caused by reservoir seiches would produce a flow/survival relationship is fully supported by the CBR model. However, the CBR model and the data indicated the break point is much lower than the ISAB suggested.

## Impacts of withdrawal on temperature and survival

Recently the effect of very large water withdrawals on smolt survival were investigated (Olsen 2003). The analysis, based on the CRiSP passage model, withdrew up to 80% of the 2001 summer flow from Hanford Reach. The analysis estimated the effect of the withdrawal on temperature using a flow/temperature relationship derived from historical data at McNary Dam. With the relationship, an 80 kcfs flow reduction from withdrawal increased river temperature by 0.8$^{o}$C. The impact on various stocks was mixed. Snake River spring chinook and steelhead stocks were virtually unaffected by Hanford withdrawals because the fish migrated prior to the July-August withdrawal period. Snake

River fall chinook were unaffected because these were transported in barges. However, fish that migrated from the Okanogan would experience a significant decrease in survival from their release point to Bonneville tailrace (survival = 2% with 0 withdrawal, survival = 0.5% with 80 kcfs withdrawal). This preliminary impact analysis suggests that survival decreases gradually with increasing withdrawals and only for stocks that directly experience the reduced flows.

### The impacts of global warming

Although the impacts of global warming on Columbia/Snake River salmon have been of interest for some time, only recently has it been possible to assess the possible impacts. A model study by Payne et al. (in press) explored the impacts of global warming on air temperature and river flow in the Columbia River system. Air temperature was projected to increase over the century by 2$^{o}$C while the annual precipitation was projected not to change (Figure 9). The model predicted that flow volume would not change, although the flow profile would shift to higher winter flows and lower summer flows as a consequence of the warming (Figure 10).

Even though future climate predictions are highly uncertain, we may surmise from this study that spring flows may be similar to what they are today but that spring temperatures may be warmer several decades in the future. In the summer, however, we may expect both the flows and temperatures to be similar to conditions in the 2001 low flow year. If these predictions were accurate, the water policies of today will have to be reconsidered. Perpetuating existing flow policies would be even more wasteful than they are currently, and would limit the ability of water managers to allocate water appropriately in a new climate regime.

## Water management and the Precautionary Principle

The current Columbia/Snake River water policies are based to a large degree on the "Precautionary Principle," which is a response to uncertainty in the face of risks to the environment. In sum, it promotes acting to avoid serious or irreversible potential harm, despite lack of scientific certainty as to the likelihood, magnitude, or causation of that harm (PPP 2003). Although the Precautionary Principle is accepted by some resource managers and is intuitively reasonable, there are problems with its application. Reliance on the Precautionary Principle has sparked major controversy, raising issues around equity, "green protectionism," conflicts between environment and development priorities, the use of sound science, and the role of stakeholders in decision-making concerning risk (PPP 2003). Of particular concern is that reliance on the Precautionary Principle diminishes the motivation to scientifically manage resources and resolve uncertainties. This trend is especially evident in Columbia River flow management. For several decades, the argument has focused almost entirely on flow alteration, increasing river flows and continued reworking of the hypothesis for how flow is the single and essential variable for water management (Anderson 2001). This approach has been protected by the Precautionary Principle. Enough information is available, and the conclusions found within that information are sufficiently certain, to discard the existing flow alteration policy.

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# Figures

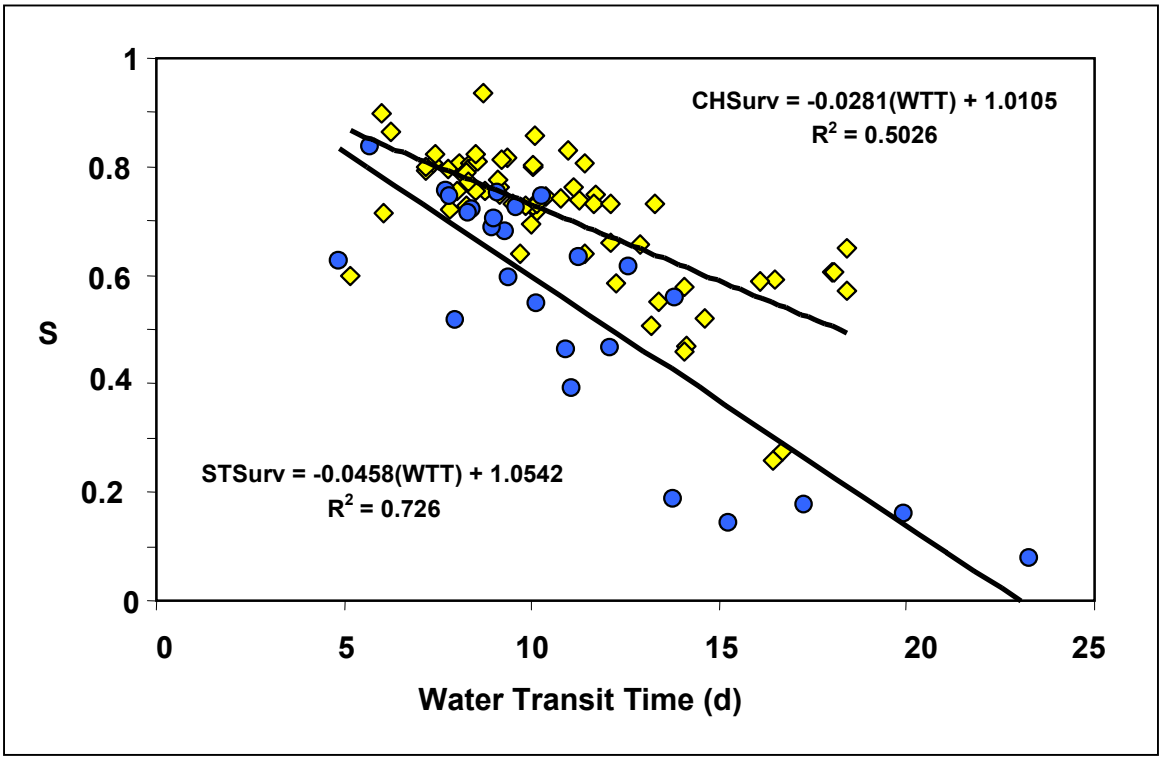


**Figure 1. CBFWA relationship between survival (S) and water transit time for Snake River spring chinook (◊) and steelhead (●). Reformatted from Petrosky et al. (2003).**

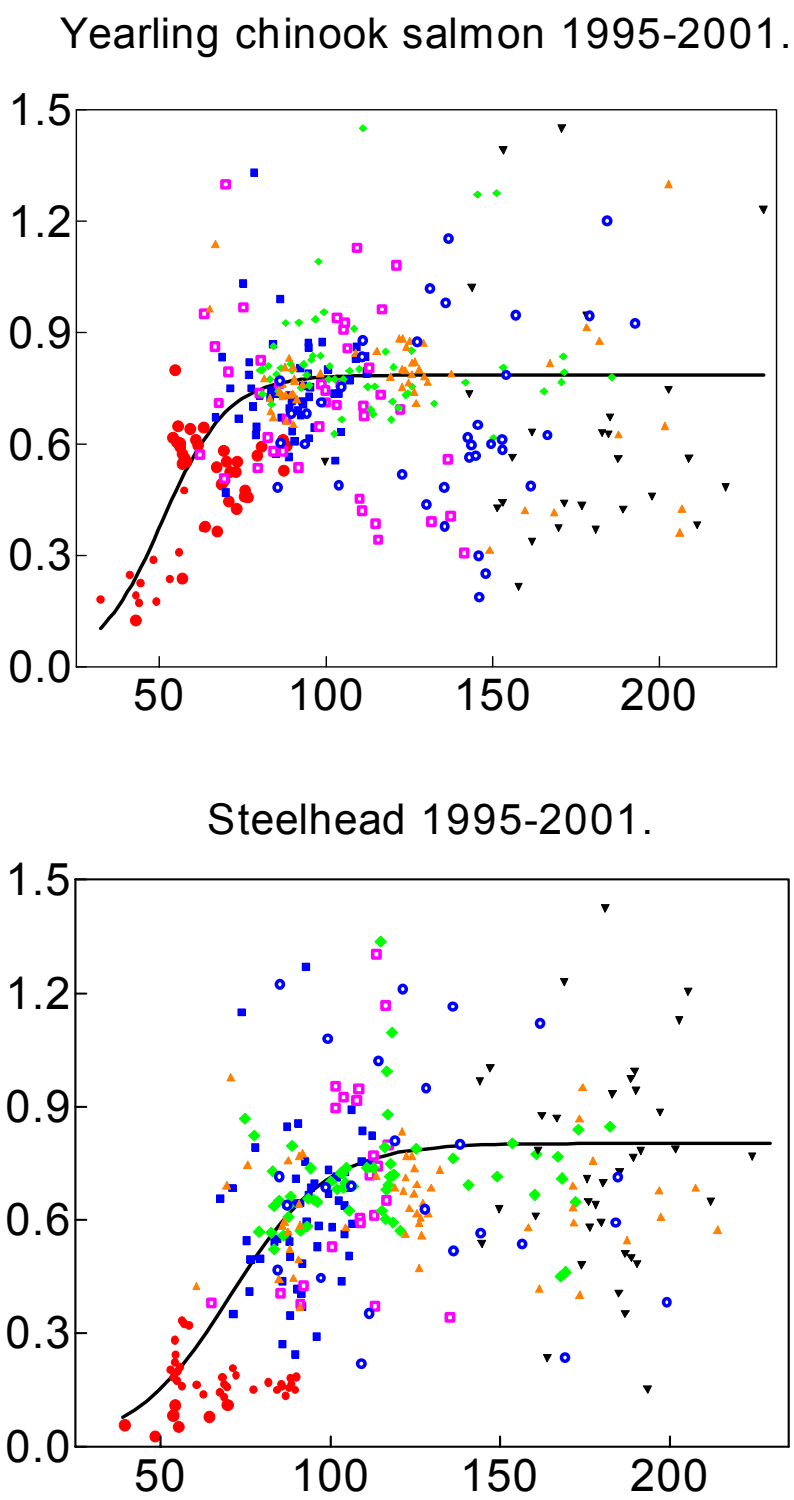


**Figure 2. NOAA analysis of flow and survival between Lower Granite Dam and McNary Dams (Williams et al. 2002).**

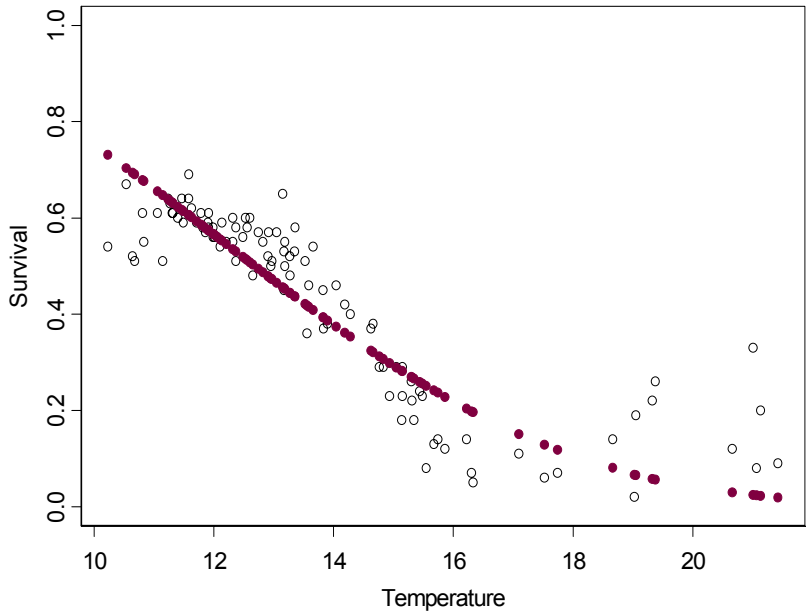


**Figure 3. CBR model showing relationship between chinook survival and temperature over the reach LGR and MCN in 2001. Survival estimated with PIT tags designated (○) survival estimated with the CBR model designated (●) (from Anderson 2003a).**

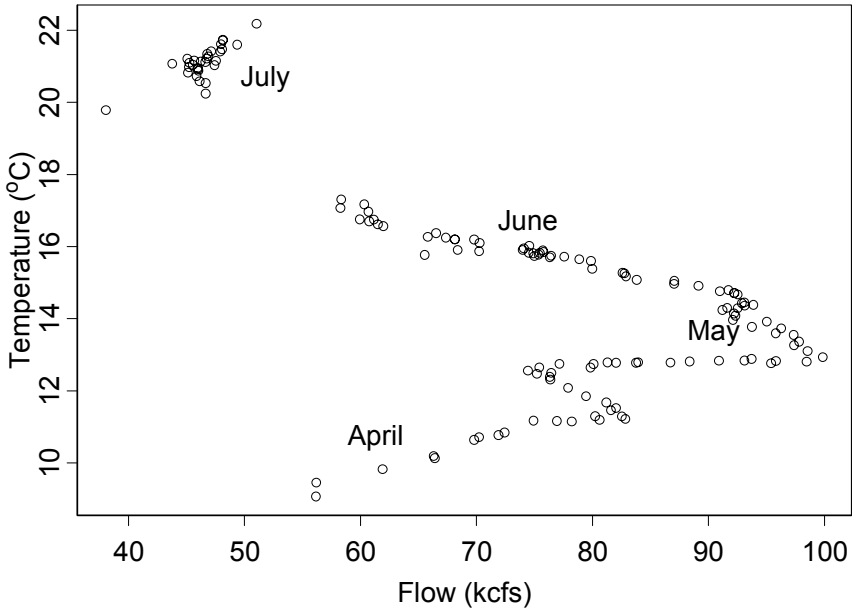


**Figure 4. Temperature flow relationship in 2001 in Snake River.**

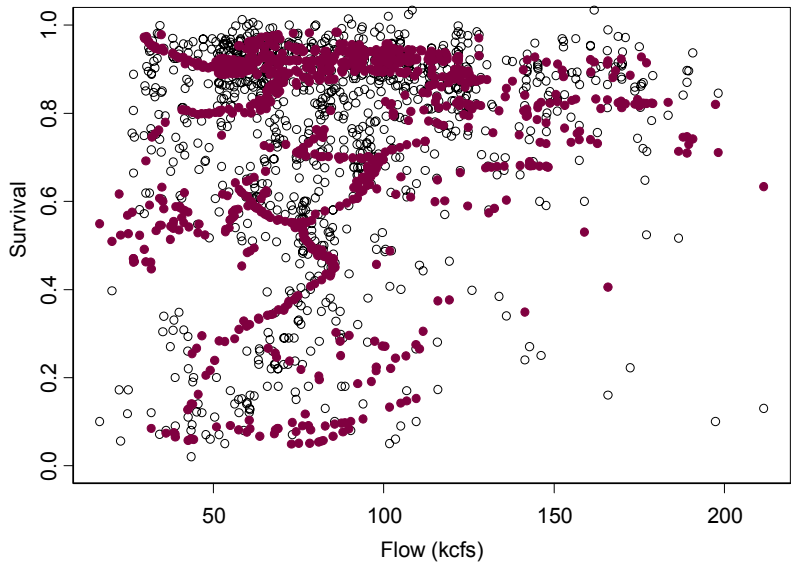


**Figure 5. Modeled and observed chinook survival vs. flow over single and multiple reaches between LGR to MCN over the years 1995-2002. Survival estimated with PIT tags designated (○) survival estimated with the CBR model designated (●) (from Anderson 2003a).**

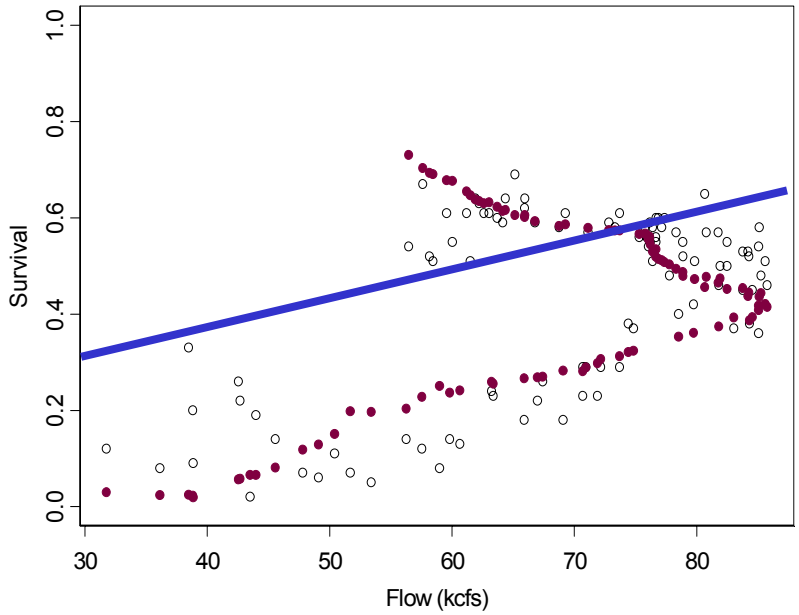


**Figure 6. Spring chinook survival vs. flow between Lower Granite Dam and McNary dam for 2001. Survival estimated with PIT tags designated (○) survival estimated with the CBR model designated (●). Line depicts the low flow segment of NOAA's hockey stick flow/survival relationship (from Anderson 2003a).**

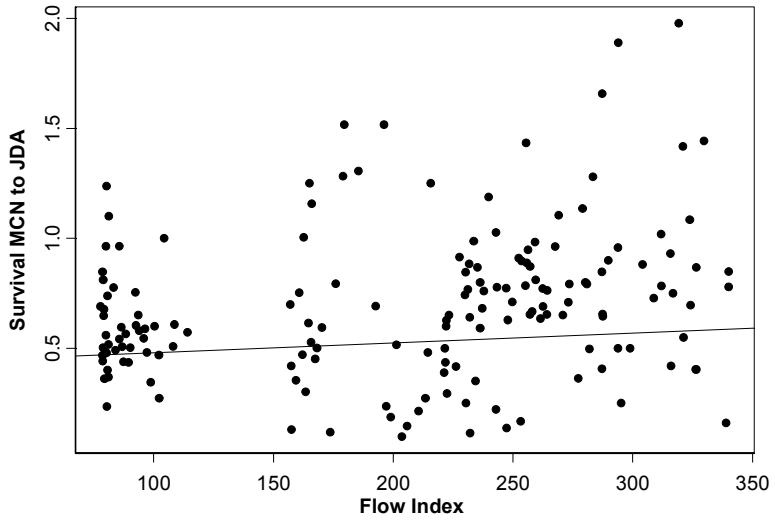


**Figure 7. Flow and survival of fall chinook passing though John Day Reservoir between June 21 and August 8 over years 1999 – 2002. Regression line is weighted by the std-err of survival.**

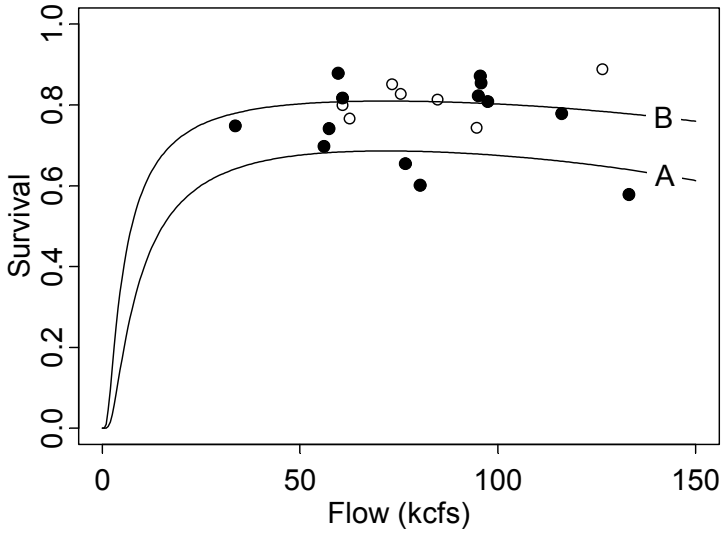


**Figure 8. Relationship of flow to smolt survival from Dworshak Hatchery to Lower Granite Dam over the years 1990 and 2001. Curve A models survival with a travel distance X = 116 km and curve B uses X = 64 km. Open points are survivals for release dates greater than Julian Day 100. Solid points are survivals for release dates Julian Day 100 or less (from Anderson 2003b).**

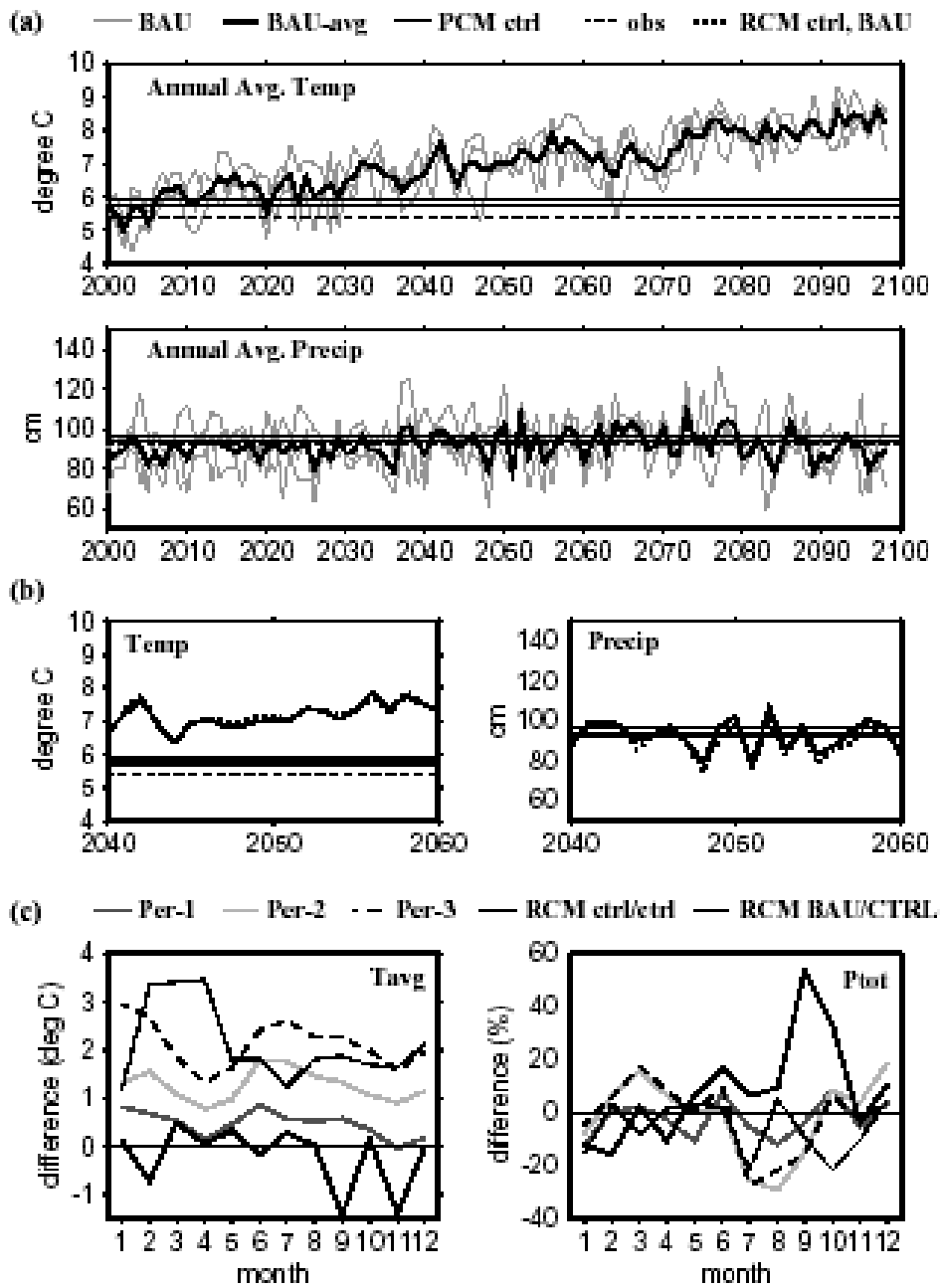


**Figure 9. (a) Downscaled PCM BAU climate PNW-average annual total precipitation and average temperature, compared with long-term averages from the PCM and RCM control climates and observations (1950-99); (b) comparison of downscaled RCM and PCM BAU-averaged climate variables (legend from (a)); and (c) CRB-average monthly total precipitation and average temperature: PCM BAU Period average changes relative to PCM control climate ("Per-1 to Per-3"), RCM BAU average changes relative to RCM control climate ("RCM BAU/CTRL"), and RCM control climate difference from PCM control climate ("RCM CTRL/CTRL") (from Payne et al. in press).**

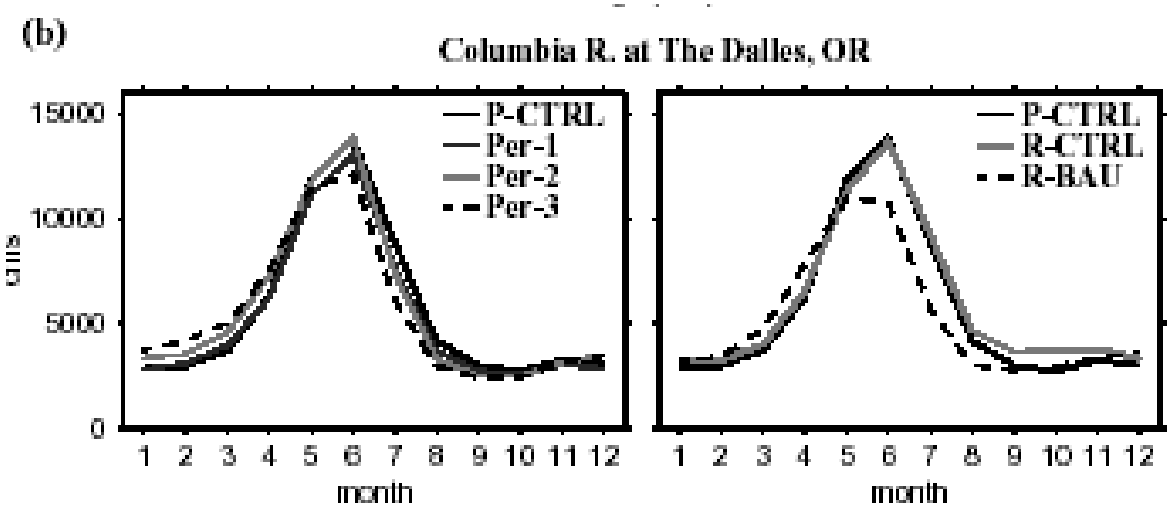


**Figure 10. Mean monthly streamflow hydrograph for the Columbia River at The Dalles, OR, for the PCM BAU ensemble average climate and RCM BAU climate, and the PCM and RCM control climate scenarios (from Payne et al. in press).**

# Attachment 3

# A Collision Theory Based Predator-Prey Model and Application to Juvenile Salmonids in the Snake River Basin

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

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2/6/2003

## 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 ~ $a$FC (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 $\tau$, 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 $\tau$, first define the chance a prey encounters a predator in traveling a short distance by the equation

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

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[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 $\lambda$ 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 $\alpha$, within which a predator and prey must simultaneously reside in order for the predator to consume the prey. Consider $\alpha$, 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 $\rho$, 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 $\rho dx$ predators (FIG. 1) and because the encounter area of each predator is $\alpha$, 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 $\omega^2$ is the sum of the variances of the predator and prey velocities.

Using Eq. (9) in Eq. (5) to define $\tau$ 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 $\omega$ can not be calculated. However, because the *b* coefficients are not statistically different from zero in all years except 1997, we may assume that $\omega$ 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, $\delta$, characterizing the average distance at which a predation event occurs can be defined

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

To estimate $\delta$, the predator density over the migration path is required. To derive a very approximate estimate of $\rho$, 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 $\lambda$, 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 $\lambda$ 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, $\sigma^2$. 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 $\omega$ 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. $\lambda$ has units of km, $\omega$ has units of cm/s. Subscripts min and max are defined by standard errors on the regression parameters.

| Year | $\lambda_{min}$ | $\lambda_{ave}$ | $\lambda_{max}$ | $\omega_{min}$ | $\omega_{ave}$ | $\omega_{max}$ |
|---|---|---|---|---|---|---|
| 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.

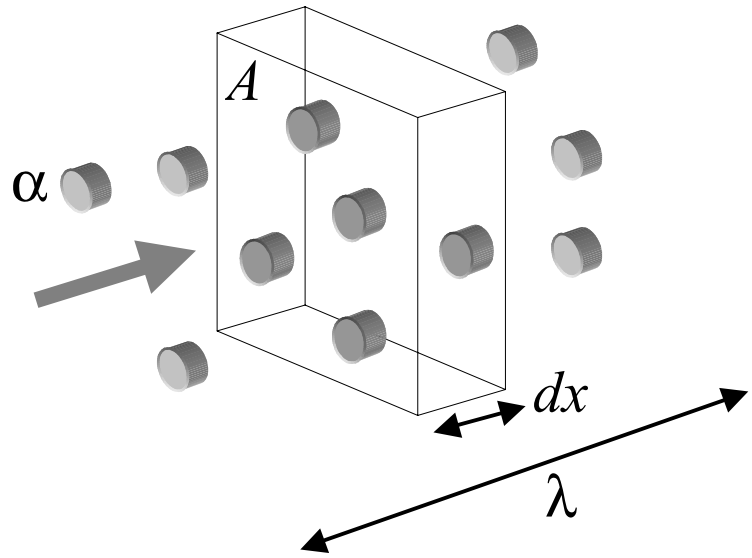


Figure 1

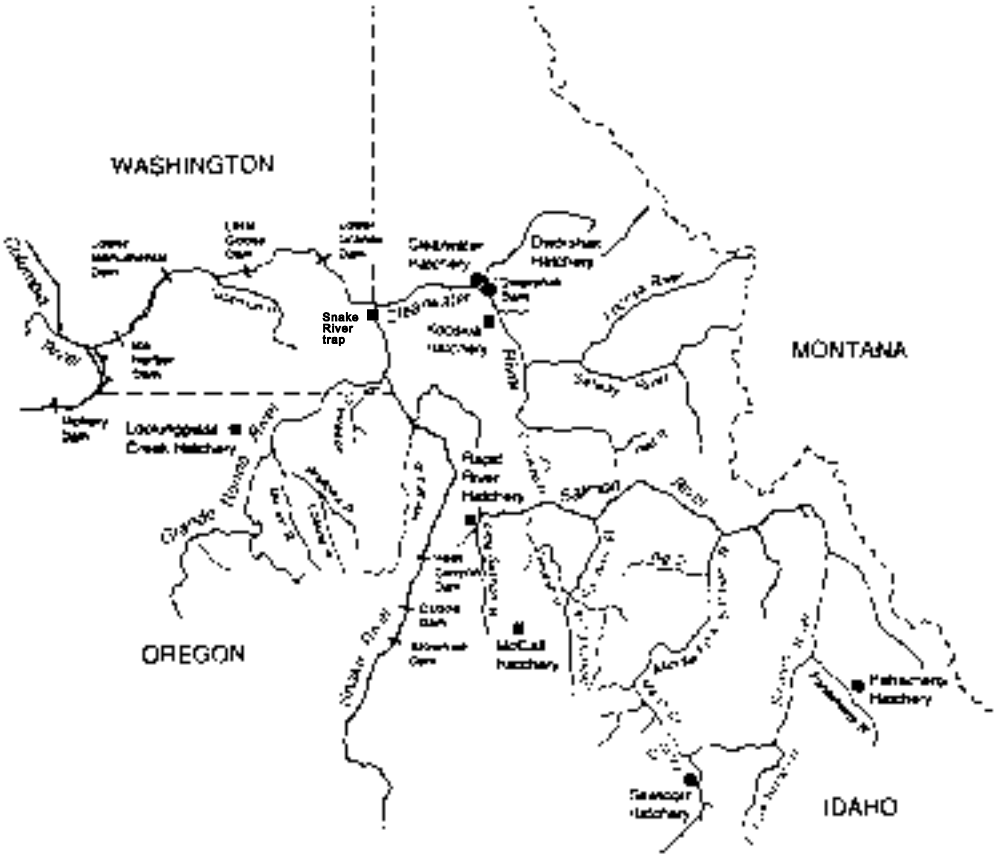
WASHINGTON
MONTANA
OREGON
IDAHO
Snake River trap
Dworshak Hatchery
Kooskia Hatchery
Rapid River Hatchery
McCall hatchery
Salmon River

Figure 2

# Attachment 4

# Mean Free-Path Length Theory of Predator-Prey Interactions: Application to Juvenile Salmon Migration

# Mean free-path length theory of predator-prey interactions: application to juvenile salmon migration

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Submitted to Ecological Modeling

January 21, 2004

**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. This simplifying assumption makes population-based models more tractable but ignores potentially important behaviors that characterize predator-prey dynamics. Here, we expand traditional predator-prey models by incorporating directed and random movements of both predators and prey. The model is based on theory originally developed to predict collision rates of molecules. The temporal and spatial dimensions of interaction between predators and prey are determined by defining movement rules and the predator's field of vision. These biologically meaningful parameters can accommodate a broad range of behaviors within an analytically tractable framework suitable for population-based models. We apply the model to prey (juvenile salmon) migrating through a field of predators (piscivores) and find that traditional predator-prey models were not adequate to describe observations. We compared model parameters estimated from mortality data of juvenile chinook salmon migrating through the Snake River in the northwestern United States to estimates derived from independent approaches and data sources and found them to be in agreement. For this system, we conclude that travel distance is more significant than travel time for the survival of a cohort of migrating prey. This finding may have implications for the use of flow augmentation to protect endangered fish species.

*Key words: predator-prey model; survival; mean free-path length; juvenile chinook salmon; migration, Snake River*

## INTRODUCTION

The first predator-prey models (Lotka, 1925; Volterra, 1926), and nearly all subsequent predator-prey models formulated in terms of differential equations, apply a law of mass action, which has its origins in chemical reaction theory first proposed by Waage and Guldberg (1864). In predator-prey models predation events are typically assumed to be analogous to the combining of molecules, such that in its simplest form the predation rate is equal to the product of predator and prey densities and a constant expressing a rate of interaction. The models have since evolved (Berryman, 1992), incorporating such refinements as predator satiation (Hollings, 1959), multi-predator and prey species (May, 1974), and dispersion and diffusion (Okubo and Levin, 2001). These improvements characterize the effective densities of predators and prey more realistically, but they ultimately use the Lotka-Volterra model mass action assumption. Models that go beyond the mass action assumption e.g., ratio-dependent models (Arditi and Ginzburg, 1989) do not allow for variability in the behavior of predators and prey.

It has been noted that the spatial scales of interactions between organisms, sometimes referred to as the "ecological neighborhood," is important in determining population dynamics (Addicott et al., 1987; Pascual and Levin, 1999). Within these local scales of interaction, the movements and distributions of predators and prey in response to each other can significantly complicate the interactions and are likely to invalidate many assumptions in simple predator-prey models (Lima, 2002). Peterson and DeAngelis (2000) address this issue by developing an individual-based model (IBM) of juvenile salmon migrating through a field of piscivores. Simulated pulses of fish move through a series of cells representing a stretch of river and within each cell there is some probability of encountering predators. The authors find that the estimated intensity of predation depends on the size of the cells (DeAngelis and Peterson, 2001). This result is useful in illustrating the importance of spatial effects and the effects of scale issues on a model. From a practical perspective, however, the appropriate cell size is not immediately evident and therefore the system dynamics depend on a free parameter with an uncertain ecological meaning. In general, IBMs can incorporate detailed behaviors and show great promise in exploring predator-prey reactions, but they are limited by difficulties in obtaining general results that can be scaled upward to the population level (Pascual and Levin, 1999; Murdoch et al., 1992).

The problem of understanding the role of local scales of interaction on population dynamics can be approached by identifying individual level behaviors that are important for determining population dynamics and incorporating these behaviors into population models. One spatially explicit model of predator-prey encounter rates was developed by Gerritsen and Strickler (1977), who characterize zooplankton encounter rates in three dimensions in terms of relative velocities and densities of zooplankton and their prey. Here, we consider this problem from a perspective somewhat similar to Gerritsen and Strickler's model, henceforth labeled GS, in which we seek to define the length scale of interaction in terms of fundamental behaviors of the interacting species. Because we are primarily interested in the survival of

migrating prey, we pay particular attention to the interaction between directed and random components of movement.

Our approach is motivated by the "mean free-path" theory, which lies at the foundations of kinetic theory as conceived by Maxwell and Boltzmann in the late nineteenth century. In the kinematic theory of gases, the collision rate between molecules depends not only on the relative magnitude of velocities but also on the degree of randomness they exhibit. An emergent property is the mean free-path length between molecular collisions (Feynman et al., 1963). We apply this theory to predator and prey populations by describing their movements in terms of both directed and random components. This allows us to distinguish predator tactics such as "cruising search" and "sit-and-wait" (Hart, 1997). As free-path length theory characterizes the mean features of a gas in terms of the small-scale properties of molecules, the theory applied to animals characterizes large-scale predator-prey dynamics in terms of the small-scale interactions of the predators and prey.

To demonstrate the practical capabilities of a mean free-path length theory (MFL), we apply the model to data on the mortality of juvenile salmon migrating through the Snake River. During their seaward migration, millions of juvenile salmon are consumed by indigenous and non-indigenous predators (Ward et al., 1995). This predation is one of several factors that determine the dynamics of salmon populations in the Columbia River Basin (NRC, 1996). Understanding the details of the predator-prey interactions is therefore of practical as well as theoretical interest. We utilize an extensive data set where several hundred thousand spring chinook salmon (*Oncorhynchus tshawytscha*) were tagged and released at several hatcheries in the Snake River Basin (Figure 1). After a migration ranging from approximately 100 to 800 km, the fish were detected at a downstream site and mortality for each release group was estimated. We test the results of the MFL model, by comparing the fitted model coefficients to independently estimated values.

Finally, we note that the GS model, which described interactions among zooplankton in explicit spherical coordinates, yields similar dynamics to the MFL model. This conclusion corroborates a result obtained by Evans (1989).

## MODEL OF PREDATOR-PREY INTERACTIONS

The assumptions of the model are as follows: 1) A prey can be described as a point in space that takes a path with mean velocity **U** and random fluctuating component $\mathbf{u}^*$; 2) Predators are likewise points with mean velocity **V** and random component $\mathbf{v}^*$. The directed components of velocity have magnitudes $U$ and $V$; 3) Predators are randomly distributed with uniform probability distribution in space with density $\rho$; 4) The scale of the predator-prey encounter volume is described by a constant cross-sectional area of interaction $\alpha$. A predation event, which eliminates the prey, occurs when a predator and prey are within a distance $r = \sqrt{\alpha/\pi}$.

Over an ensemble of prey and predator-prey interactions, the average time between encounters is $\tau$ and the probability of a single encounter follows a Poisson distribution such that

$$\text{probability of predator encounter in time} = \exp(-t/\tau) \tag{1}$$

where $t$ is the total exposure time. This is also an expression of the survival over time. To derive an expression for $\tau$, first define the chance a prey encounters a predator in traveling a short distance as

$$\text{probabilty of predator encounter in distance } = \frac{\Delta x}{\lambda} \tag{2}$$

where $\lambda$ is the prey's path length and $\Delta x$ is a small distance in the direction the prey travels.

Similar to the mean free-path length in molecular collisions (Feynman, et al., 1963), the chance of encounter can also be expressed in terms of the fraction of a unit encounter area occupied by predators. Consider a plane of unit area, $A_{unit} = 1$, that is perpendicular to the relative average movement between the prey and its predators (Figure 2). Over a short distance of its path $\Delta x$, the prey sweeps out a small volume $A_{unit}\Delta x$. This volume contains $n$ predators where $n = \rho A_{unit}\Delta x$. The area of the plane covered by predators is $A_{predator} = \alpha n = \alpha\rho A_{unit}\Delta x$ where $\alpha$ is the encounter area of a predator-prey interaction. The encounter area can be expressed in terms of the encounter distance, $r$, at which a predation event occurs, so $\alpha = \pi r^2$. The chance of encountering a predator traveling the small distance $\Delta x$ is equivalent to the area occupied by the predators divided by the unit area of the plane, which is simply

$$\text{probability of predator encounter in } \Delta x \quad = \pi r^2 \rho \Delta x \tag{3}$$

Equating equations (2) and (3) the path length is

$$\lambda = \frac{1}{\rho \pi r^2} \tag{4}$$

The encounter time and path length are related by $w$, which is the magnitude of the relative speed of the prey with respect to the predators. Thus, $\lambda = w\tau$ and the characteristic encounter time is

$$\tau = \frac{1}{\rho \pi r^2 w} \tag{5}$$

The relative speed, which we designate the encounter speed, is expressed as a root-mean-square (*rms*) speed between the predator and prey as

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

Next, represent prey and predator velocity vectors in terms of their average and fluctuating parts as

$$\mathbf{u} = \mathbf{U} + \mathbf{u}^* \quad \text{and} \quad \mathbf{v} = \mathbf{V} + \mathbf{v}^* \tag{7}$$

where **U** and **V** are the mean prey and predator velocity vectors and $\mathbf{u}^*$ and $\mathbf{v}^*$ are the associated fluctuating or random velocity vectors about the mean vectors. This decomposition into mean and fluctuating parts is commonly used in kinematic studies and in hydrodynamics (Sverdrup et al., 1942). By our definition, the fluctuating components are uncorrelated and have zero means, and so the expected value of the square of the difference between the velocity vectors is

$$E\left[\left(\mathbf{v}-\mathbf{u}\right)^2\right]=E\left[\mathbf{U}^2\right]-E\left[2\mathbf{UV}\right]+E\left[\mathbf{V}^2\right]+E\left[\mathbf{u}^{*2}\right]+E\left[\mathbf{v}^{*2}\right] \tag{8}$$

The *rms* encounter speed defined by equation (6) reduces to

$$w=\sqrt{W^2+\omega^2} \tag{9}$$

where the squared *mean* encounter speed is

$$W^2=V^2+U^2-2UV\cos\theta \tag{10}$$

where $V$ and $U$ are the deterministic magnitudes of vectors **V** and **U** respectively, $\theta$ is the angle between the mean paths of the predator and prey, and the mean squared *random* encounter speed is described in terms of the variances of fluctuating magnitudes of $\mathbf{v}^*$ and $\mathbf{u}^*$ as

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

Note that $\omega^2$ is the sum of the variances of the fluctuating or random parts of the predator and prey speeds and it admits any distribution for the fluctuating velocities as long as the mean values are zero.

Using equation (9) in equation (5) to define $\tau$ in equation (1), the probability of a prey encountering a predator over time, which is also equivalent to the prey survival over time, is

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

From equation (12) we can express the rate of predation in the form of traditional predator-prey equations as

$$\frac{dS}{dt}=-\pi r^2\rho S\sqrt{W^2+\omega^2} \tag{13}$$

where $\rho$ and $S$ are the predator and prey population densities. Thus, the rate coefficient, $\pi r^2\sqrt{W^2+\omega^2}$, is equivalent to the time constant in a Lokta-Volterra (Lotka, 1925; Volterra, 1926) predator-prey equation with a dimension of $t^{-1}$. However, here the rate term is specified in terms of the predator's ecological neighborhood as characterized by an encounter length scale $r$, and the behaviors of the predators and prey are characterized by the mean and *rms* random encounter speeds, $W$

and $\omega$. With visual predators, $r$ should depend on the range of visibility in the environment, the sensory ability of the predators, and the near field probability of a predator's chance of capturing a prey. The encounter speeds characterize the probabilities of predator-prey encounters over space and time.

The model, in the form of equation (12) or (13) has characteristics not found in a formulation in which the rate coefficient is simply a constant. For example, because the predation rate depends on the mean and random speeds of the predator and prey, the predator's foraging rate is explicitly coupled to its energy expenditure, and so the optimal foraging strategy for the predator may depend on the character of the prey's speed. This issue was explored by Gerritsen (1984) for the case of random free-swimming aquatic animals. In addition, prey survival over time and space depends on the relative motions of predators and prey. Some special cases illustrating the effect of behaviors on the survival equation are discusses below.

*Special cases of prey survival*

The general MFL model can be further simplified to a number of simple cases in which the predators and prey have different deterministic and fluctuating motions that are germane to ecological situations.

If prey migrate through a corridor or field of resident predators, then by definition the predator mean speed is zero ($V = 0$), and by definition of the prey's migration behavior, its deterministic speed, is simply its average migration velocity, $U$. Then the average prey migration time $t$, distance $x$, and velocity are related by $x = Ut$, and equation (12) simplifies to

$$S = \exp\left( -\frac{1}{\lambda}\sqrt{x^2 + \omega^2 t^2} \right) \tag{14}$$

Equation (14) will be referred to as the *XT model* because survival depends on both the distance traveled and the travel time. The relative importance of migration distance and time on prey survival depends on the random encounter velocity $\omega$. The length scale $\lambda$ is a measure of distance between predator-prey encounters and from equation (4) it depends on the encounter length scale and the predator density as

$$\lambda = 1/\pi r^2 \rho \tag{15}$$

Whereas, the $x$ term in the equation could equally be replaced with $Ut$, the dependence on $x$ is appropriate for characterizing the survival of animals as they migrate over fixed distances. In this case, the importance of migration velocity, i.e. travel time over a fixed distance, in determining the prey's survival depends on the magnitude of the random encounter speed $\omega$ relative to the average migration velocity. To illustrate the importance of migration velocity, we rewrite equation (14) as $S = \exp\left( -\frac{x}{\lambda}\sqrt{1 + (\omega/U)^2} \right)$ and plot $S$ vs. $U/\omega$ for migration over an arbitrary distance $x = \lambda$ (Figure 3). This results in a hockey stick like survival response vs. prey migration rate expressed in multiples of the random velocity. The break, at which

survival becomes essentially linear with migration velocity, occurs when the migration velocity drops below the random encounter velocity, i.e. when $U \leq \omega$.

If the prey migration is rapid, so the predators are essentially stationary relative to the prey's migration velocity, then $U^2 \sim W^2 \gg \omega^2$. In this case, prey that move with different average migration velocities experience the same survival probability over a fixed migration distance even though their migration times may be different over the distance. Under these conditions, the asymptotic form of prey survival depends on distance as

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

Equation (16) will be referred to as the *gauntlet model* and over a fixed migration distance survival is independent of the prey's velocity. Although the average travel time is related to survival through the average velocity, the equation $S = \exp\left(-Ut/\lambda\right)$ is not a suitable description of survival in a gauntlet model since both velocity and travel time are required to characterize survival and their product is simply the migration length $x$. In this case, survival simply decreases exponentially with distance traveled and is independent of the amount of time it takes to travel the distance.

If predators and prey are both mobile and resident within the habitat, then $W$ = 0 and we obtain a traditional *exposure model*

$$S = \exp\left(-\frac{\omega}{\lambda}t\right) \tag{17}$$

Note the survival over time depends on the predation length scale characterized by $\lambda$, and the intensity of the predator-prey interactions as characterized by $\omega$. In this case, survival declines exponentially with exposure time $t$. Although the GS model and equation (17) have different mathematical forms, both assume prey and predators only have random movement. In addition, they have virtually identical characteristics (Appendix A).

In these special cases, the specific rate of prey mortality, defined $\left(1/S\right)dS/dt = f\left(\bullet\right)/\lambda$, depends on the reciprocal of the predator length scale $\lambda$ and a rate function $f\left(\bullet\right)$ that characterizes the rate of predator-prey encounters. The length scale depends on the number of predators in the habitat and the predator-prey encounter distance $r$. The encounter rate function characterizes the rate at which predators and prey interact, which in turn depends on their behaviors. In the gauntlet model, each predator encounters an individual predator at most once while in the exposure model multiple encounters are possible.

## A CASE STUDY WITH MIGRATING JUVENILE SALMON

We apply the model to data on the survival of juvenile salmon during their seaward migration. Each year during their migration through the Snake and Columbia Rivers and their tributaries, millions of juvenile salmonids are consumed by predators

(Rieman et al., 1991). The major piscivores are the native northern pikeminnow (*Ptychocheilus oregonensis*) and three non-indigenous species - smallmouth bass (*Micropterus dolomieu*), walleye (*Stizostedion vitreum*) and channel catfish (*Ictalurus punctatus*) (Poe et al., 1991). In addition, birds consume migrating juvenile fish. Notably predation by the Caspian tern (*Sterna caspia*) has increased over the past decade as a result of a substantial increase in their population (Roby et al., 1998).

These predators are generalists that feed seasonally and may employ different tactics, so our application of the model to the survival data reflects a mixture of different foraging strategies by predators. However, the model is flexible and accommodates a variety of behaviors. Ultimately, the fact that we know the fate of thousands of prey after migrating past a field of predators yields a rich data set for our analysis.

We use mark recapture studies conducted on Snake River system. Between 1993 and 2003, 287 tagged groups of spring chinook were released from 17 hatchery located in the tributaries of the Snake River Basin (Figure 1). The fish, tagged with passive integrated transponder (PIT) tags (Prentice et al., 1990), were released from locations in the Snake River tributaries ranging from 31 km to 772 km upstream of the detection site at Lower Granite Dam. Release sample sizes ranged from 6 to 51,196 fish with a median release size of 796 fish. Fish were released between days of the year 71 through 130 and in general fish released further upstream tended to be released earlier (Figure 4). Survivals to Lower Granite Dam were estimated with the multiple–recapture model for single-release groups (Muir et al., 2001).

The relationship between log survival and the migration travel time was variable from one year to the next (Figure 5). Individually, only 1996, 1997, 1998, 2001 and 2002 exhibited significant ($p < 0.01$) linear regressions of log($S$) vs. $t$, which were weighted by the standard error of $S$. Correlations were typically low with only 1993 and 1995 exhibiting $r^2 > 0.5$. No relationship between log survival and travel time was evident for all years combined ($r^2 = 0.08$, $P < 0.0001$). A stronger and consistent relationship was evident between log survival and migration distance (Figure 6). Weighted regressions of log($S$) vs. $x$ were significant ($p < 0.005$) for all years except 1997. The $r^2$ correlations were above 0.7 for 6 of the 10 years and the regression of all years combined was very significant ($r^2 = 0.65$, $P < 0.0001$). Migration velocities increased with release site distance from Lower Granite Dam. An unweighted linear regression gave $u$ (cm/s) = 1.4 + 0.026 $x$ (km) ($r^2 = 0.70$, p-value < 0.0001). However, there was no relationship between release day and migration velocity ($r^2 = 0.03$, p-value < 0.0019).

Similar results were found in other studies. Muir et al. (2001), analyzing a subset (1992 through 1998) of the data used in our analysis, noted that the estimated survival from the hatcheries was inversely correlated with migration distance to Lower Granite Dam ($r^2 = 0.64$, $p < 0.001$). In a linear regression, survival also had a weak inverse relationship with travel time to Lower Granite Dam ($r^2 = 0.17$, $p > 0.07$). Studies have also noted that survivals of juvenile salmon migrating through the Columbia and Snake Rivers were significantly related to the distance traveled but not to travel time (Bickford and Skalski, 2000; Smith et al., 2002).

To apply the MFL model to the PIT tag data, we note that the juvenile salmon rapidly migrate through the tributaries while the predators are resident within the tributaries. Therefore, equation (14) is an appropriate form of the MFL model for fitting the juvenile salmon survival data. To estimate the model parameters, we write equation (14) in a multiple-linear form

$$\left(\log S\right)^2 = ax^2 + bt^2 \tag{18}$$

where the parameters are defined

$$\lambda = 1/\sqrt{a} \quad \text{and} \quad \omega = \sqrt{b/a} \tag{19}$$

Because of the large difference in sample sizes, we weighted the individual survival estimates by one over the square of the standard error of the survival and fit equation (18) to each year and to the combined years (Table 1).

Equation (19) requires that $a > 0$ zero and $b \geq 0$, otherwise the model coefficients are imaginary. However, the regression puts no constraints on the values of *a* and *b*. This is somewhat problematic if the random speed, ω, is near zero then *b* is also be near zero and may take on a negative value as a result of estimation error. Therefore, we also calculate λ and ω using regression coefficients *a* and *b* plus and minus their standard errors (se). We pair the estimates of *a* plus its standard error with estimates of *b* minus its standard error because *a* and *b* vary inversely in equation (18). That is, if due to estimation error the point estimate of *a* is low, then we expect that the point estimate of *b* will be high. In Table 2, NA indicates imaginary estimates of ω.

## RESULTS

The $r^2$ of the XT model fit to data over the years 1993-2003 range from 0.54 to 0.97, the fit to all years is 0.65, and the p-values are significant at the 0.005 level or greater for all years (Table 1). Estimates of the λ range between 354 and 917 km and estimates of ω range between 0.5 and 12 cm/s. Including all years together, the encounter velocity is less than 0.6 cm/s and the mean free-path length is 454 km. In some years, because *b* is negative, the random encounter velocity ω cannot be calculated, but in all years except 1996 the upper estimate of ω can be calculated. An estimate of ω is not possible in 1996 because *b* is negative and the standard error is less than the absolute value of *b*. However, λ is not affected by this negative *b* estimate in 1996. Regressing log *S* against *x* gives λ = 354, which is identical to λ obtained by equation (18) that includes the negative *b*. We conclude that in 1996 ω = 0, which implies survival is best characterized by a gauntlet process of equation (16).

## COMPARISON WITH INDEPENDENT PREDICTIONS

To evaluate the model, we compare parameters estimated from the XT model to estimates derived from other methods using independent observations.

*Encounter distance*

From equation (4), the predation encounter distance, $r$ , characterizing the average distance at which a predation event occurs can be written

$$r = 1/\sqrt{\pi\rho\lambda} \tag{20}$$

To estimate $r$, the predator density over the migration path is required. To derive a very approximate estimate of $\rho$, 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 (National Marine Fisheries Service, 2000, www.nwfsc.noaa.gov/pubs/white/whiteflow.pdf) 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 $x10^6$ $m^3$, the predator density approximation is $\rho$ = 7.9 $x10^{-5}$ predators $m^{-3}$. Using the range of the mean estimates of $\lambda$ from Table 2, the predator-prey encounter distance varies between 6.6 and 10.7 cm with the estimate for the combined years of $r$ = 9.4 cm. Because $\lambda$ 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 on average 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 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 disk readings in Lower Granite Reservoir typically vary between 10 and 50 cm (Columbia River DART, 2002, www.cbr.washington.edu/dart/). 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 et al., 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 the reaction distances estimated above. Consequentially as has been found in other systems (Gregory and Levings, 1998), we may expect that in the Snake River tributaries water visibility may be an important determinant of predator-prey encounter distance and therefore of juvenile salmon survival.

*Random encounter velocity*

The predator-prey random encounter velocity depends on the random prey velocity, $u^*$, and the random predator velocity, $v^*$, according to equation (11). An upper estimate of $u^*$ 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, $u$, and a spread term, $\sigma^2$. The travel time distribution is inversely related to the migration velocity distribution and, based on Tweedie (1957), the variance in the migration velocity is

$$Var(x/t) = \frac{u}{x}\sigma^2 + \frac{2}{x^2}\sigma^4 \tag{21}$$

where $x$ is the migration distance. The square root of equation (21) provides an upper estimate of $u^*$. From four years of data, 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, an average velocity over the ground was 7 cm/s in the tailrace and 1 cm/s in mid-reservoir (Martinelli and Shively, 1997; Martinelli et al., 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 12 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 equation (21) contains additional elements other than the actual random swimming velocity. Equation (21) is derived from a difference in arrival times of fish after traveling the distance $x$. Because early in migration juvenile salmon 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 equation (21) should represent an upper limit of $u^*$. Considering these caveats, XT model's estimate of $\omega$ on the order of a few cm/s is reasonable.

## DISCUSSION

Our model, based on the theory of mean free-path length of molecular collisions, extends the mass action principle characterization of predator-prey dynamics. In doing so, we added more realism to population-based predator-prey

models by accommodating behaviors usually only found in individual-based models. Accordingly, the model represents basic properties of the ecological neighborhood in which predators and prey interact, including the mean and random velocities of the predator and prey, the predator-prey encounter length scale, akin to the predator's visual field of perception, and the predator density. Applying the model to an extensive data set of juvenile salmon prey migrating through predators in the Snake River, we estimated the prey's mean free-path length and the random predator-prey encounter velocity. As a check on the model, we estimated the model parameters from independent data. The predator encounter length scale, derived from predator density and the prey's mean free-path length, was close to the predator's visual field during the migration. Estimates of the random encounter velocity from observations of the predator and prey movement agreed with the model estimated random encounter velocity. The fact that our estimated parameters are consistent with those obtained from independent, behavioral studies demonstrates the feasibility of the model.

Characterizing appropriate spatial and temporal scales is important to understanding predator-prey interactions (Levin, 1992; Murdoch et al., 1992; Pascual and Levin, 1999). Although there is no single approach, in our model, small scales of a predator-prey ecological neighborhood (meters and seconds) emerge from prey survival data on the scale of kilometers and days. This result illustrates that the nature of the small-scale events affects the large-scale patterns.

Just because our broad-scale based results are consistent with behaviors occurring at a much finer scale, it does not necessarily confirm that the model accurately captured these behaviors – other behaviors at the scale of the ecological neighborhood might produce similar results at the population level. However, the MFL model does have a simple institutive basis. For example, prey survival being distance dependent when passing a gauntlet of stationary sit-and-wait predators and being time dependent when the predators roam the environment, makes sense. If the predators are fixed, each predator only gets one chance at an individual prey and if the predators search, multiple encounters are possible. Furthermore, since the nature and rate of predation depends on the predator and prey movements, the mean free-path length approach naturally encompasses foraging energetics and therefore has the potential to explore whether sit-and-wait or search foraging strategies are more energetic under a given prey behavior and flux through a habitat. Finally, the model may have implications to problems of diffusion of organisms since the theory suggests that the rates of diffusion of the predators or prey could affect the encounter rate and therefore the prey survival rate. Further studies are required to explore the implications of the theory and whether or not predictions are realistic and meaningful. However, we can reasonably conclude that simple predator-prey dynamics that ignore the processes occurring on the scale of the ecological neighborhood and which express survival only as a function of exposure time, do not adequately represent the predator-prey system we examined. Thus, ignoring behaviors on the fine scale can produce erroneous predictions on the broad scale.

The model fit to data on the survival of juvenile spring chinook salmon migrating though the Snake River produces a random encounter velocity near zero, which suggests in effect that fish pass a gauntlet of predators such that travel distance,

not travel velocity, is a major factor determining survival. This finding is significant to actions being taken to recover the endangered salmon chinook species in the Snake River. Currently the Biological Opinion directing actions for the recovery of the endangered spring chinook identifies a flow target to speed the fish through the river system (NMFS, 1995; NMFS, 1999a; NMFS, 1999b; NMFS, 2000). This flow target is achieved by release on the order of 2 million acre feet of storage water from the Snake River reservoirs during the juvenile migration (Olsen et al., 1998). Our analysis suggests a mechanistic basis for the observation (Smith et al., 2002) that fish migration survival is not correlated with river flow and fish migration velocity.

Our initial impetus to develop this model was based on our interest in the conservation biology of Pacific salmon and the consistent observation that simple exposure-time models cannot be reconciled with a considerable body of survival data. Thus, we specifically tailored the model to predict survival rates of the prey. Alternatively, because the theory in essence only expands mechanisms defining the rate coefficient, it can be incorporated into predator-prey models of greater complexity to include predator satiation and energetics, predator and prey diffusion, or multiple species interactions. In this formulation, we could determine whether alternative strategies employed by the predators yield long-term consequences on the dynamics of the two populations. Further, since different search strategies require different expenditures of energy, our basic model could also be recast in an optimal foraging framework.

## ACKNOWLEDGEMENTS

We are thankful to the Bonneville Power Administration for funding this project through the Columbia Basin Research, School of Aquatic & Fishery Sciences, University of Washington, Seattle, Washington.

## APPENDIX A: COMPARISON WITH THE GS MODEL

The Gerritsen and Stricker (1977) predator-prey encounter model for zooplankton is similar to the MFL model in that both characterize a relative speed between predators and prey and describe predation in terms of an encounter distance. Here we illustrate the similarity between the GS model and equation (17) and corroborate a result obtained by Evans (1989).

The GS model assumes uniform distributions of predator and prey moving randomly in a 3-dimensional field. The model characterizes the frequency of interaction using a spherical polar coordinate reference frame. The predator and prey have swimming velocities $v$ and $u$ respectively and their relative speed is

$$w = \sqrt{u^2 + v^2 - 2uv\cos\theta} \tag{22}$$

where $\theta$ is the angle of prey relative to the angle of the vector $\mathbf{v}$ of the predators motion. Assuming the prey and predators are randomly distributed, the encounter rate of a prey to predators in the GS model is

$$\frac{1}{S}\frac{dS}{dt}=\frac{\pi r^2\rho}{6}\frac{\left(\bar{u}+\bar{v}\right)^3-\left|\bar{u}-\bar{v}\right|^3}{\bar{u}\cdot\bar{v}} \tag{23}$$

where $\bar{u}$ and $\bar{v}$ are the mean speeds of the predator and prey populations. The equivalent encounter rate in the MFL model is

$$\frac{1}{S}\frac{dS}{dt}=\pi r^2\rho\sqrt{E\left(u^{*2}\right)+E\left(v^{*2}\right)} \tag{24}$$

Note that the mean speeds in the GS model are equivalent to the *rms* speeds in the MFL model such that $\bar{u}=\sqrt{E\left(u^{*2}\right)}=u_{rms}$. Thus, the formulations of the encounter rate by the equation (23) for the GS model and (24) for the MFL model are different. Furthermore, in the GS formulation the mean speeds are deterministic, while in the MFL model speeds have probability distributions with intensities characterized by the *rms* speeds. The encounter rates for the case with probability distributions in the animals' speeds were numerically calculated by Gerritsen and Stricker. On average, equation (23) underestimates the encounter rates by about 1 to 10% depending on the distributions assumed for the predator and prey speeds. However, even though the formulations are different, their characteristics are virtually identical. This is illustrated in Figure 7, which compares the encounter rates of the two equations for differing predator and prey speeds. Note that in the deterministic form of the GS model, encounters rates are between 0 and 5% lower than the rates of the MFL model. This is the same level of under prediction Gerritsen and Strickler determined when comparing the deterministic speeds form of the GS model to a numerical form in which the predator and prey speeds were normally distributed.

We conclude that the MFL model is a simpler expression than the GS model and that it provides a close fit to the deterministic form of the GS model. The MFL model agrees even more closely with the numerical form of the GS model using randomly distributed predator and prey speeds.

In a brief discussion of the GS model, Evans (1989) simplifies the GS relative encounter rates and includes a turbulent term that is functionally equivalent to the random velocities with the important distinction of being for both predator and prey. He concludes that the values obtained for encounter rates differs from the GS model by no more than 6%, corroborating the result obtained above.

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Table 1. Regressions coefficients for equation (18) coefficients for spring chinook hatchery releases and migration to Lower Granite Dam over the years 1993-2003. "n" is the number of release groups.

| Year | n | r-sqr | *a* ($10^{-6}$ km$^{-2}$) | | *b* ($10^{-5}$ d$^{-2}$) | |
|---|---|---|---|---|---|---|
| | | | estimate | std-err | estimate | std-err |
| 1993 | 17 | 0.94 | 3.11 | 0.34 | -3.21 | 13.78 |
| 1994 | 38 | 0.97 | 4.76 | 0.21 | 6.22 | 11.79 |
| 1995 | 43 | 0.80 | 7.25 | 1.00 | 24.35 | 28.08 |
| 1996 | 15 | 0.97 | 7.96 | 0.44 | -18.04 | 4.60 |
| 1997 | 12 | 0.68 | 1.56 | 1.46 | 20.66 | 9.28 |
| 1998 | 15 | 0.88 | 1.32 | 0.27 | 9.45 | 3.70 |
| 1999 | 22 | 0.54 | 1.19 | 0.40 | 4.76 | 2.85 |
| 2000 | 43 | 0.60 | 1.34 | 0.39 | 6.73 | 2.39 |
| 2001 | 26 | 0.81 | 1.93 | 0.43 | 6.21 | 2.27 |
| 2002 | 26 | 0.86 | 5.19 | 0.87 | -2.97 | 5.43 |
| 2003 | 25 | 0.78 | 6.91 | 1.00 | 0.20 | 5.07 |
| All years | 287 | 0.65 | 4.85 | 0.25 | -1.85 | 2.12 |

Table 2. Model parameter ranges. $\lambda$ has units of km, $\omega$ has units of cm/s. Subscripts min and max are defined by standard errors on the regression parameters. NA indicates an estimate not computable because of a negative *b* estimate

| Year | $\lambda_{max}$ | $\lambda_{ave}$ | $\lambda_{mim}$ | $\omega_{max}$ | $\omega_{ave}$ | $\omega_{min}$ |
|---|---|---|---|---|---|---|
| 1993 | 601 | 567 | 539 | 5.0 | NA | NA |
| 1994 | 469 | 458 | 449 | 5.3 | 3.1 | NA |
| 1995 | 400 | 371 | 348 | 7.3 | 5.0 | NA |
| 1996 | 365 | 354 | 345 | NA | NA | NA |
| 1997 | 3131 | 800 | 575 | 12.0 | 9.9 | 7.4 |
| 1998 | 975 | 871 | 794 | 8.6 | 7.3 | 5.7 |
| 1999 | 1127 | 917 | 793 | 6.9 | 5.5 | 3.5 |
| 2000 | 1026 | 864 | 761 | 7.1 | 6.1 | 4.9 |
| 2001 | 815 | 719 | 651 | 5.7 | 4.9 | 3.9 |
| 2002 | 481 | 439 | 406 | 1.9 | NA | NA |
| 2003 | 412 | 381 | 356 | 2.4 | 0.5 | NA |
| All years | 466 | 454 | 443 | 0.6 | NA | NA |

# Figure

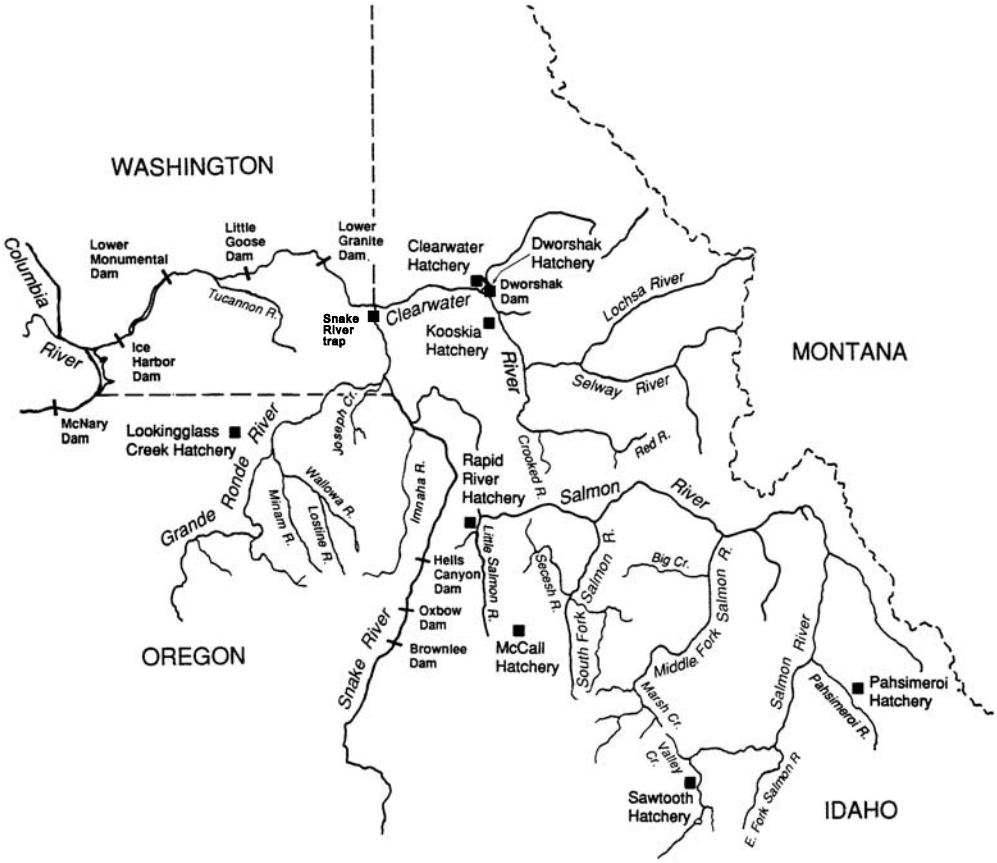


Figure 1. Map showing Snake River tributaries and the hatcheries from which fish were released for survival studies.

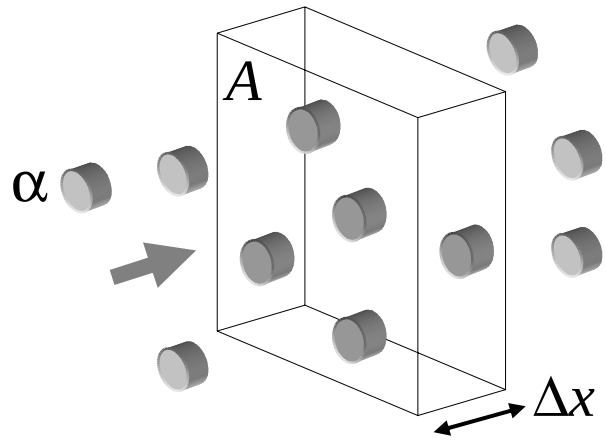


Figure 2. Illustration of a prey (arrow) moving a distance Δx through a unit area *A* of predator habitat. Predators (cylinders) have a cross-sectional area α. The probability of encountering a predator while traveling Δx is equal to the fraction of the unit area covered by predators

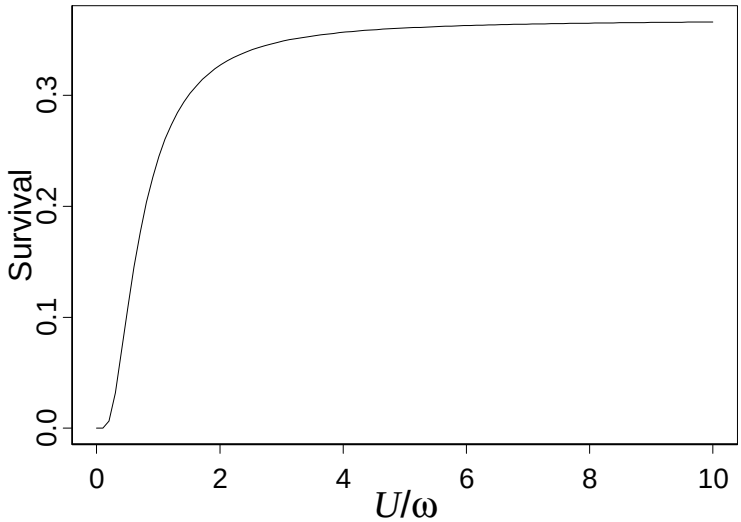


Figure 3. XT model survival vs. average migration velocity *U* divided by the random component of the velocity ω.

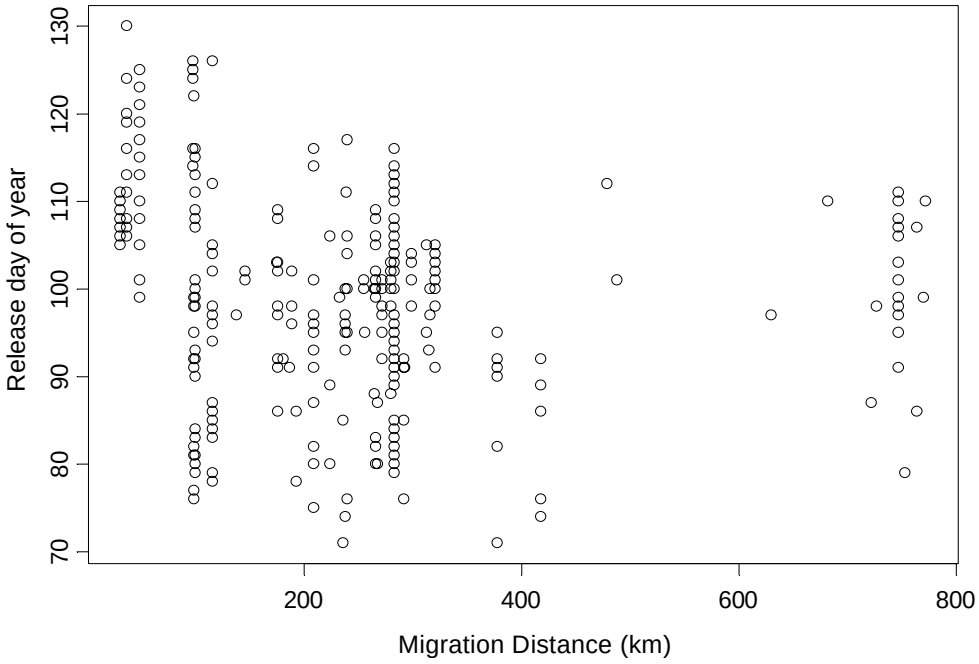


Figure 4. Tag group release day of year vs. distance of migration to Lower Granite Dam.

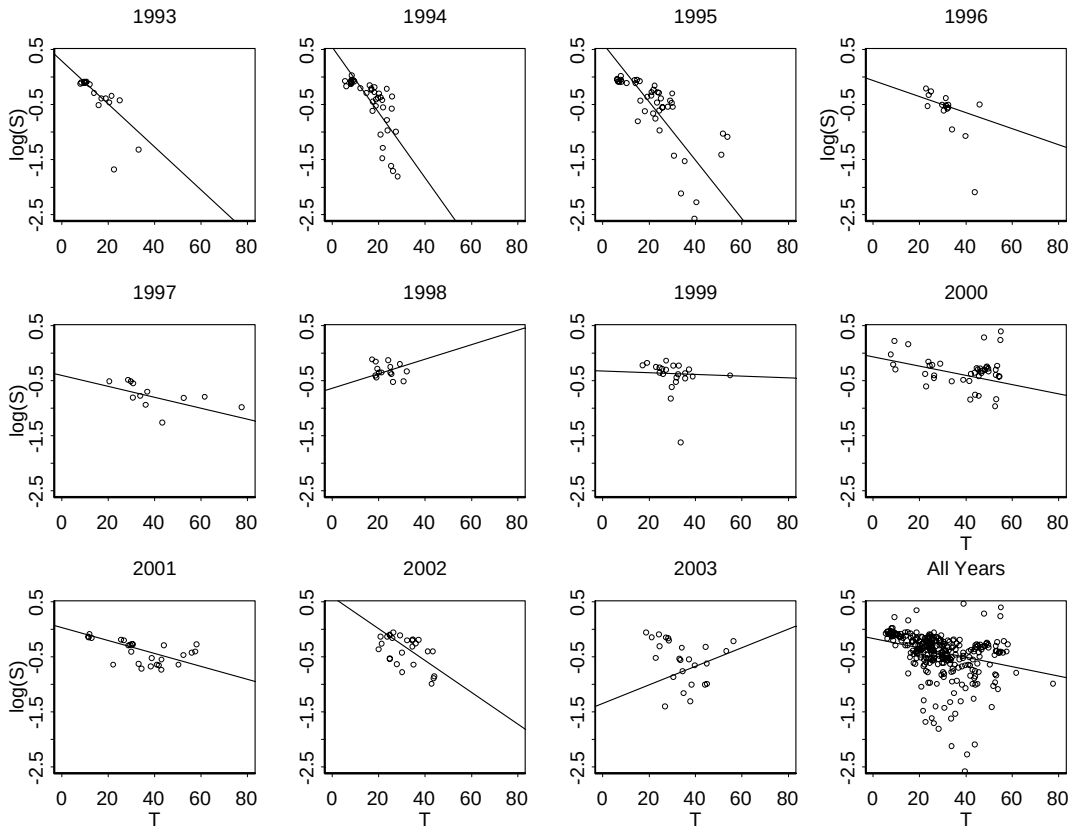


Figure 5. Regression of long survival, log(*S*), vs. migration travel time, *T* (d). Regressions are weighted by $1/se^2$ of *S*.

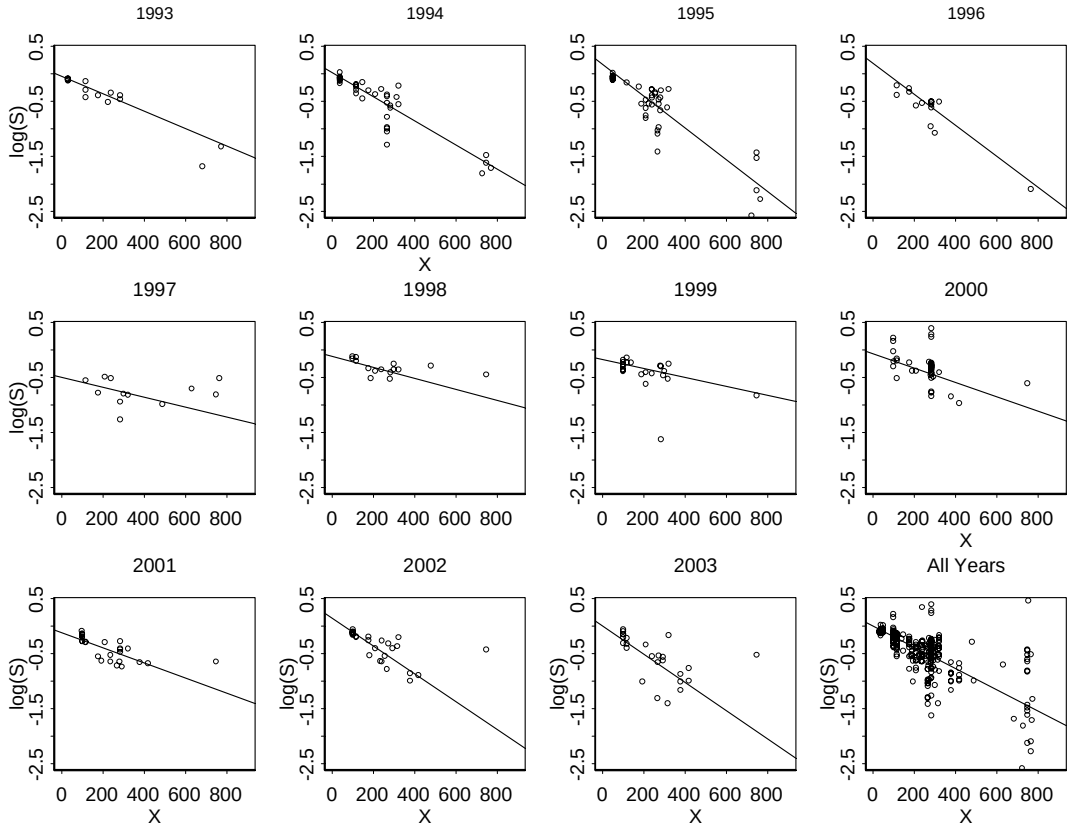


Figure 6. Regression of log survival, log(*S*) vs. migration distance, *X* (km). Regressions are weighted by $1/se^2$ of *S*.

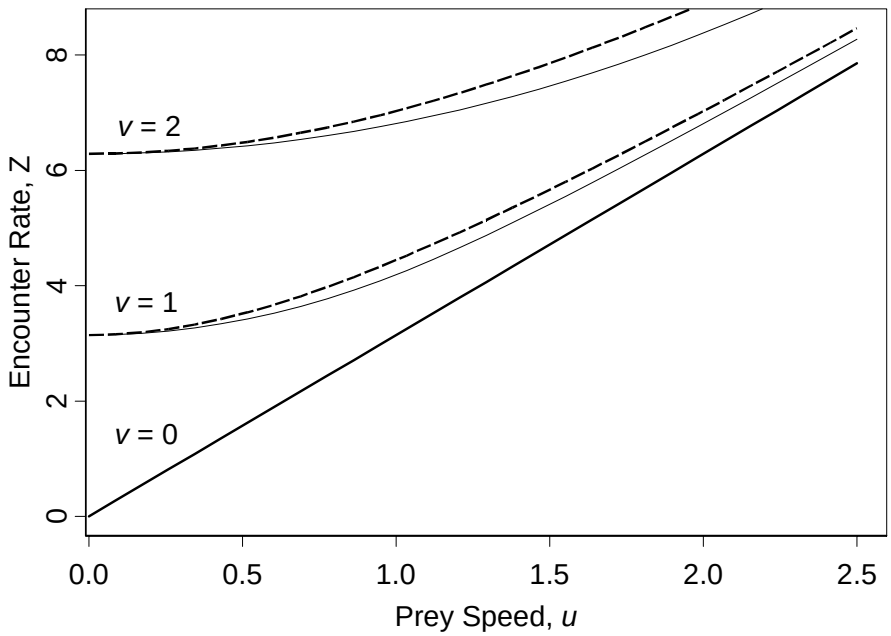


Figure 7. Comparison of encounter rate of predators by prey as function of prey and predator speeds for the GS model ( ── ) and the MFL model ( — — ).