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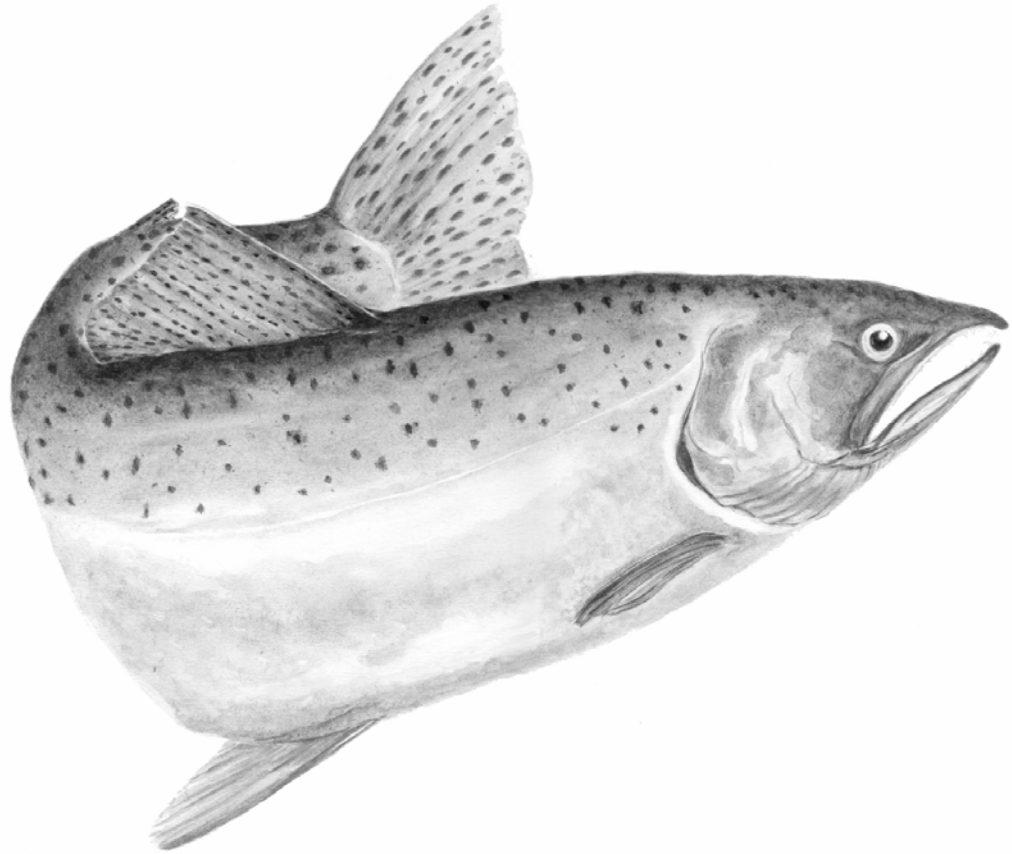
Latent Mortality Report



Review of Hypotheses and Causative Factors Contributing to Latent Mortality and their Likely Relevance to the "Below Bonneville" Component of the COMPASS Model

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Executive Summary

On November 27, 2006, NOAA Fisheries requested that the ISAB review a number of hypotheses about the causative factors that contribute to latent mortality. Additionally, the Columbia River Inter-Tribal Fish Commission urged the ISAB to agree on a method for assigning weights to the submitted hypotheses. These hypotheses are intended for incorporation in the Comprehensive Passage (COMPASS) model, specifically to affect the "below Bonneville" component of the model. In an effort to provide the modeling team with some initial input, the ISAB offers the following recommendations and conclusions:

- The ISAB recommends that the various components of latent mortality be merged into a single model. A merged data set should be used to evaluate this model with a statistical analysis that aids in selecting among hypotheses. The ISAB recommends this investigation as the most scientifically rigorous approach to reducing the number of alternative hypotheses based on all available data.

- The ISAB concludes that the hydrosystem causes some fish to experience latent mortality, but strongly advises against continuing to try to measure absolute latent mortality. Latent mortality relative to a damless reference is not measurable. Instead, the focus should be on the total mortality of in-river migrants and transported fish, which is the critical issue for recovery of listed salmonids. Efforts would be better expended on estimation of processes, such as in-river versus transport mortality that can be measured directly.

- Estimates based on limited time series have a high degree of uncertainty, and ocean conditions that affect survival will vary on several time/space scales. Thus there will be considerable uncertainty in estimates of post-Bonneville survival, and the ISAB recommends that this uncertainty be accounted for as efforts to reduce it continue. Estimates of the uncertainty should be bounded and incorporated in simulation models and annual management planning processes.

- Future monitoring and research is needed to further quantify biological factors that contribute to variability in estimated post-Bonneville mortality. In particular, the ISAB recommends that acoustic tags continue to be developed and used to assess and partition mortality in the lower river, the estuary, and the Pacific Ocean shelf. In addition, the ISAB recommends the continuation of PIT tagging with a monitoring and evaluation program designed to reduce the current levels of uncertainty.

- The ISAB also recommends that a logit modeling approach be investigated as a potential alternative framework for future modeling of post-Bonneville mortality.

Assignment

The downstream passage (LGR → Bon) part of the COMPASS model is nearing completion, and it is time to turn attention to the estuarine, ocean, and return phases (Bon → Ocean → Bon → LGR). The ISAB received a request from NOAA Fisheries (27 November 2006) to review a pantheon of competing hypotheses about the causative factors that contribute to latent mortality. In a separate memo, the Columbia River Inter-Tribal Fish Commission (4 December 2006) urged the ISAB to agree on a method for assigning weights to the submitted hypotheses. These hypotheses are likely to affect the "below Bonneville" component of the COMPASS model, once provision for it is included. These disparate hypotheses are neither mutually consistent nor exhaustive, so how should latent mortality be incorporated into the COMPASS model? In an effort to provide the modeling team with some initial input, NOAA Fisheries posed questions that should influence the latent mortality modeling effort.

1. How plausible is each of the latent mortality hypotheses, based on the lines of evidence presented by the authors (e.g., data, analyses based on those data, and other considerations)? Are the data appropriate for deriving the estimates of interest?

2. How applicable is each of the hypotheses to estimating the overall (absolute) latent mortality associated with the existence of dams and current/recent operations? How does each rank in this regard? Is sufficient information available for the ISAB to suggest how the hypotheses should be weighted in this type of application?

3. How applicable is each of the hypotheses for estimating changes in latent mortality associated with alternative operations? Among all hypotheses how does each rank with respect to providing plausible estimates? Is sufficient information available for the ISAB to suggest how the hypotheses should be weighted in this type of application?

4. To what extent are the hypotheses and methods described applicable to ESUs other than Snake River spring/summer Chinook salmon? Is information presented or referenced that permits such inferences? (Please consider all 13 listed ESUs in the Columbia River basin).

5. Can the ISAB suggest modifications to any of the hypotheses and analyses to make them more useful? Would these changes affect the rankings or weightings?

6. What lines of future research and monitoring would be most valuable for reducing the uncertainty associated with the magnitude of, and mechanisms responsible for, latent mortality?

Introductory Comments

From examining the general life-cycle information for wild Snake River spring/summer Chinook, we have some data regarding survival estimates and mechanisms of mortality for the early part of the life cycle down to just below Bonneville Dam. Briefly, direct mortality is that which occurs directly from some event along the downriver passage through (or around) the hydropower system, i.e., mortality directly associated with the hydrosystem (Figure 1). We denote that mortality as $L_{I,ds} = (1 - S_{I,ds})$ for the fish that run the entire eight project in-river gauntlet, with $S_{I,ds}$ being the survival rate from LGR →BON. Similarly, $L_{T,ds} = (1 - S_{T,ds})$ is the direct mortality of transported fish. Both $S_{I,ds}$ and $S_{T,ds}$ are estimable with Cormack-Jolly-Seber (CJS) methods, and both can be, and have been, included in the downstream module of COMPASS.

In considering the subsequent fate of fish that have arrived below Bonneville, the authors of the questions posed above define "latent mortality associated with the FCRPS (for Snake River fish) as any mortality that occurs after fish pass Bonneville Dam as juveniles that would not occur if the FCRPS dams did not exist." We assume that latent mortality pertains only to fish that originate above Bonneville and not to effects of changes in the hydrograph below Bonneville. Unfortunately, there is no direct information on *latent mortality* for the *damless* reference condition, and we cannot make this definition operational.

Survival estimates are lacking for segments below Bonneville to the estuary, within the estuary to the ocean, within the ocean, and on the return to Bonneville Dam, but we do know that post-Bonneville mortality of Columbia River fish is high, as reported from SARs (smolt to adult ratio, the ratio of returning adults to outmigrating smolts) in the literature. The big question is how much of this mortality is due to pre-Bonneville factors (L_i) that may show up as mortality in locations below Bonneville, and how much is due solely or primarily to factors inherent in those habitats and the life cycle of these salmonids.

Numerous factors have been postulated or documented regarding this post-Bonneville mortality, only some of which are related to the FCRPS:

- Predation by birds, especially Caspian Terns and cormorants
- Predation by pikeminnow and marine fishes (hake)
- Increased vulnerability to predators because of size, stress, or disease
- Timing of ocean entry
- Ocean conditions, including density dependent factors, upwelling, spring transition, ENSO and PDO
- Ocean interceptions and harvest of returning adults
- In-river adult pre-spawn mortalities (harvest, dam passage, marine mammals, disease, high temperatures)

Several alternative approaches have been proposed to investigate relative latent mortality for different populations of fish.

1. Estimate the latent mortality that is incurred by fish that have run the entire in-river gauntlet of eight dams and compare that with the latent mortality that is incurred by fish that have been transported.

2. Compare latent mortality for upriver populations versus downriver populations, such as comparing Snake River versus John Day populations.

3. Compare latent mortality for pre-dam populations versus post-dam populations.

4. Use environmental conditions as covariates to account for changes in latent mortality.

None of these approaches can provide **direct** estimates of absolute latent mortality for the damless reference condition although attempts to do so have been made by invoking additional strong, unverifiable assumptions.

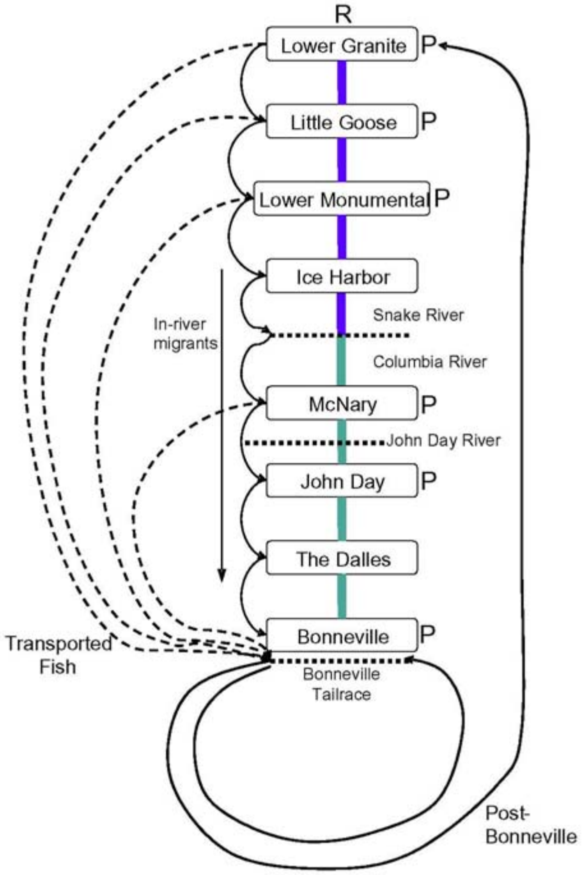

Figure 1. Features of the Snake and Columbia River Hydrosystem that are modeled in COMPASS for Snake River fish. "R" represents the release site or the site where the fish enter the hydrosystem (head of Lower Granite reservoir). Fish move downstream via in-river migration or by transportation. "P" represents PIT-Tag detection sites. The post-Bonneville component of the model takes fish from the Bonneville tailrace and returns them to either Bonneville Dam or Lower Granite Dam, depending on the hypothesis.

The COMPASS document suggests no separation of transported fish into those coming from each of the four projects (Lower Granite, Little Goose, Lower Monument and McNary; Figure 1), ranging from the furthest upriver dam to the fifth dam in the system. A juvenile transported from McNary has already run the gauntlet through four upriver projects, and demographic attrition has already taken a toll on the cohort released above Lower Granite. Fish transported from Lower Granite, on the other hand, avoid all of the subsequent in-river mortality losses on the way to Bonneville. Fish transported from Little Goose or Lower Monument would also have their own histories (Budy et al., 2002).

Data indicate that Snake River wild stream-type Chinook salmon have lower smolt to adult return rates than John Day River wild stream-type Chinook salmon (Schaller and Petrosky, *in review*). One interpretation is that fish from John Day, having navigated fewer dams, survive better. Similarly, the subbasin from which the smolts were transported might also matter for subsequent (*latent*) survival, because smolts transported from different subbasins have different ages, nutritional conditions, predation histories, and arrival times below Bonneville.

Latent mortality is here defined as *the delayed effect of the downstream passage experience*, so we seek in-river passage predictor variables that we can measure. But if variation in latent mortality only exists below Bonneville, any connection between downstream passage variables and a survival signal that we can detect on the return run has been filtered and attenuated. Predictors (or surrogates) are observable in-river, but those in the ocean are not directly observable. Any signal we can detect will be subtle at best and confusing at worst, contributing to the confusion over latent mortality.

Alternative Hypotheses/Models

The competing hypotheses represent a range of ideas about latent mortality, as well as the contrast between L_I and $L_{T;}$ those hypotheses translate into different modeling strategies. Most of the discussion has been couched in terms of L_I, but the COMPASS team also has to model L_T. These two constructs are connected through D_{IT}, the ratio of SAR for transported fish to that of in-river fish.

The notation for these components follows. The Smolt to Adult Survival Rate (SAR) is the fraction of smolts that have arrived below Bonneville that eventually return as adults to the reservoir above Lower Granite, denoted as $SAR_{I,\,Bon \rightarrow LGR}$ for smolts that have run the eight-dam gauntlet and as $SAR_{T,\,Bon \rightarrow LGR}$ for smolts that have been transported from one of four upriver dams to a release point below Bonneville. We describe latent mortality as a component of these two SAR variables,

$$SAR_{I,\,Bon \rightarrow LGR} = S_{e/o} \bullet (1 - L_I) \bullet S_{I,us} \text{ for the in-river fish },$$

$$SAR_{T,\,Bon \rightarrow LGR} = S_{e/o} \bullet (1 - L_T) \bullet S_{T,us} \text{ for the transported fish },$$

and can define a SAR ratio D_{IT} as,

$$D_{IT} = \frac{SAR_{T,\,Bon \rightarrow LGR}}{SAR_{I,\,Bon \rightarrow LGR}} = \frac{(1 - L_T) \bullet S_{T,\,us}}{(1 - L_I) \bullet S_{I,\,us}}$$

Ocean survival ($S_{e/o}$) is modeled to be the same for both in-river and transported smolt, ascribing any difference to differences in latent mortality ($L_I \neq L_T$). Assuming $S_{e/o}$-values for in-river and transported fish are equal seems dubious, particularly when we know that in-river and transported fish have different survival rates from LGR →BON. However, given the assumption that $S_{e/o}$ cancels in the definition of D_{IT} above, we are still left to consider the possibility that returning adults that have matured from in-river and transported smolts might have different survival rates ($S_{I,us}$ and $S_{T,us}$) on the upstream part of their journey. We can measure $(1 - L_T) \bullet S_{T,us}$ and $(1 - L_I) \bullet S_{I,us}$ as products, but a clean estimate of the ratio $(1 - L_T) \div (1 - L_I)$ requires either strong belief in estimated upstream survival rates ($S_{T,us}$ and $S_{I,us}$) or a plausible assertion (assumption) that they are equal. An up-stream passage comparison by Berggren et al. (2006) found differences in estimated $S_{I,us}$ and $S_{T,us}$ values. Given the data available, it seems unlikely that $S_{e/o}$ is equal for in-river and transported fish.

The following comments represent the ISAB's sense of each of the hypotheses, garnered from the 8 December 2006 briefing and from the voluminous documentation submitted in support of the alternatives.

Hypothesis A – Annual L_i is a function of water travel time (WTT) for wild Snake River spring/summer Chinook

The authors of this hypothesis (Petrosky et al., 2006) used linear multiple regression to relate third year survival (S3) of Snake River spring/summer wild Chinook salmon to WTT and two ocean variables the September Pacific Decadal Oscillation (PDO) index and the April upwelling index. Water travel time (WTT) is a measure of the average number of days for water particles to travel from the confluence of the Clearwater and Snake rivers to Bonneville Dam (from April 15-May 31) and WTT was about 2 days for this period in the damless river and now with 8 dams has increased to an average of about 19 days with a range of 10 to 40 days (Petrosky et al., 2006). Estimates of S3 were derived using methods similar to Zabel et al. (2006), assuming that survival during the second and third ocean years is fixed at 0.8. The simplest best-fit model used WTT, September Pacific Decadal Oscillation (PDO) index, and the April upwelling index as predictor variables:

$$-\ln(\mathrm{S3}) = \beta_0 + \beta_1 \bullet \mathrm{WTT} + \beta_2 \bullet \mathrm{Sept(PDO)} - \beta_3 \bullet \mathrm{Apr(Upwelling\ Index)} + \varepsilon$$

Estimates of L_I are embedded within estimates of S3 but this is not the same as latent mortality with reference to the damless river.

Hypothesis B – Seasonal L_i is a function of arrival timing at Bonneville Dam for wild spring/summer Chinook

The authors of this hypothesis (Scheuerell and Zabel, 2006) used logistic regression to estimate post-Bonneville SAR of in-river migrants as a function of day of arrival below Bonneville and a year-effect. By shifting the observed distribution of arrival times forward and doing some comparative analyses they were then able to determine the percent increase in SAR versus the overall shift in arrival timing. This approach used PIT tagged fish data and the response variable was binary based on whether a fish was (1) or was not (0) detected as an adult. The relationship to latent mortality with reference to the damless river is lacking.

Muir et al. (2006) also provide some data, which give insight into the arrival timing and sources of mortality for stream-type Chinook in the lower Columbia River and estuary (i.e. below Bonneville to the mouth of the river). They investigated the arrival timing and lengths of transported (barged) and run-of-the-river fish to examine if there were differences in SARs. Muir et al. (2006) concluded that the most parsimonious explanation for differential post-hydropower system mortality of transported Chinook salmon smolts related not to effects of stress but to differential size and timing of ocean entry. They found that transported smolts were more vulnerable to predation by northern pikeminnow, *Ptychocheilus oregonensis*, in freshwater habitats and by Pacific hake, *Merluccius productus*, in marine habitats than were migrants; this was particularly true for the smaller wild smolts transported early in the season.

Hypothesis C – The existence and operation of the four Snake River dams results in annual L_i averaging 59-64% for wild Snake River spring/summer Chinook

This hypothesis/analysis estimates (Petrosky et al., 2006) annual latent mortality for wild spring/summer Chinook at an average of 59-64% based on differences in SARs from up-river (Snake River) vs. down-river (John Day) comparisons. These values represent an estimate from Deriso et al. (2001) and an updated value in Schaller and Petrosky (2006). Petrosky et al. (2006) reviewed estimates of L_I in different time periods (pre-1970 vs. post-1975) and in different locations (Snake River populations versus downstream populations), as reported by Peters and Marmorek (2001), with a mean of 0.59. A comparison of Snake River versus downstream John Day spring Chinook, forced to navigate fewer projects, yielded an average of 0.67. The year-to-year variation was quite substantial for both series. The authors indicate that cumulative stress from passage associated with the four lower Snake River dams is the primary basis for this L_i.

The stress response in juvenile salmonids has been well documented physiologically (measured by elevated levels of serum cortisol, plasma glucose, and lactate) and behaviorally. Laboratory studies simulating stress upon dam passage (multiple acute handling stressors) determined that juvenile salmonids stressed by simulated dam passage were more vulnerable to predators than non-stressed controls (Mesa 1994). The stress response for fish has also been shown to be a natural response and recovery of predator avoidance abilities/behavior has been observed to return in ~ 15 to 90 minutes (Mesa, 1994; Olla and Davis, 1989). While it is likely that multiple passage stresses occur, there is no direct measure of its leading to latent mortality because evidence to date is primarily from laboratory studies.

In a recent radio telemetry study conducted in the lower Columbia River by Schreck et al. (2006), the authors hypothesized that stress, disease, and bird predation interacted. They also suggested that juvenile Chinook stressed by their passage through the hydrosystem were more vulnerable to disease and were relatively less ready for seawater life, as estimated by relatively low gill Na^+,K^+-ATPase activity that also made them more susceptible to predation. The hatchery Chinook salmon used by Schreck et al. (2006) were on average ≥ 28 mm larger than wild fish. However, comparisons of smoltification (n=6 fish) and disease (n=8 fish) were based on very small numbers of fish sampled on the bird colony and compared different cohorts of fish including Snake River fish from the barge, fish from the bypass at Bonneville Dam where few Snake River fish were likely present, and fish of unknown origin on the bird colony.

Hypothesis D – Annual L_I is low, confounded with other variables, and unquantifiable for wild Snake River spring/summer Chinook.

This hypothesis states that L_i is not measurable. Furthermore, after a review of available research, the authors conclude if hydro-related latent mortality exists it is very low. Geiselman et al. (2006) describe the hypothesis in detail, while Paulsen and Fisher (2006), Hinrichsen (2006), Scheuerell and Williams (2005) provided information illustrating the considerable difficulties of measuring $L_{I.}$ The central idea here is that hydro-related latent mortality (L_I) cannot be derived from existing spawner-recruit data. As noted above, in the absence of survival data from the *damless* river condition, there is no **direct** way to measure L_I. Geiselman et al. (2006) conclude that observed differences in SARs and spawner-recruitment estimates**:** (1) are explainable by processes other than latent mortality, (2) are net effects – confounded with direct mortality estimates and other non-hydro life stage stresses, and (3) are traceable to overly parameterized models.

Hypothesis E – Annual D_{IT} Based on Historical D Estimates

This hypothesis asserts that the ratio of annual transported SAR to in-river SAR (D_{IT}) can be expected to remain consistent with historical D_{IT}-values observed since the mid-1990s. The modeling suggestion would be to use an annual D_{IT} that is sampled from the historical distribution of annual D_{IT}-values from medium/high flow years for any year projected to have medium/high flow. For years projected to have low annual flow, one would use the annual D_{IT} from 2001, a low-flow year.

Alternative methods of calculating historical D_{IT}-values include: (a) the method used for the Comparative Survival Study (CSS, 2006), (b) the method used by NMFS in various reports (Williams et al., 2005), and (c) the method used by the University of Washington in their ROSTER model (Buchanon et al., 2006). These methods differ in the nature of the control and transported groups, analytical methods, and temporal scale of estimates. In all of these variations, D_{IT} differs from latent mortality with reference to the damless river.

Hypothesis F – Annual Project-Specific D_{IT} Are Estimated

This hypothesis specifies that SARs should be seasonally predictable for each project. Wilson (2006) describes a method for predicting the seasonal SAR ratios (TIRs) prospectively, based on log-normal distributions derived from PIT-tag data from recent years for transported and in-river SARs. Annual, project-specific estimates of D_{IT} are obtained by removing sampling error from TIR data for both wild spring/summer Chinook and wild steelhead. Then, D_{IT} can be calculated from project-specific TIRs, measured to the release point below Bonneville.

For COMPASS modeling, TIR-values for each species, project, and year could be drawn randomly from an appropriate log-normal distribution, using project-specific parameters based on past data. We note again that $D_{IT} = (1 – L_T) \div (1 – L_I)$ differs from latent mortality, $L_{I,}$ with reference to the damless river.

Hypothesis G – Seasonal D Based on Arrival Time Below Bonneville.

For this hypothesis, Scheuerell and Zabel (2006) employed logistic regression to estimate the post-Bonneville SARs for both in-river and transported smolts. The best model included the Julian day of arrival below Bonneville Dam, a year-effect, and transportation site-effect (for transported fish only). In this model, both in-river migrants and transported smolts were considered, allowing the computation of $D_{IT} = (1 – L_T) \div (1 – L_I)$, and transported fish were separated by site of collection.

The evaluation of transported smolts was based on migration years 1995 and 1998-2002, whereas the in-river data were based on migration years 1998-2002. Based on the SAR_I and SAR_T estimates, Scheuerell and Zabel (2006) then obtained seasonally adjusted estimates of D_{IT} for the five years in common (1998-2002).

Hypothesis H – Seasonal SAR Ratios

This hypothesis incorporates seasonal changes in spring/summer Chinook values of TIR at Lower Granite Dam. Past work by CSS and NOAA suggests that transport SAR to in-river SAR ratios (TIRs) may vary in a roughly predictable way within the course of the (spring) migration season. This leads to the question of when within a season to transport wild yearling-migrant Chinook that are collected at Lower Granite Dam (LGR). Paulsen (2005) divided the migration season into quartiles and developed confidence intervals around quartile TIRs by bootstrapping PIT-tag data for migration years 1995-2003.

One Additional Hypothesis

At the request of the Council, the ISAB examined/reviewed a hypothesis proposed by David Welch. This hypothesis was examined and discussed at the CSS workshop in 2004 and is reported in the CSS Report (Marmorek et al. 2004). This hypothesis states that *The hydrosystem indirectly affects smolt-to-adult survival (SARs) by shifting the timing of mortality of transported fish to post Bonneville Dam, based on the hypothesis that fish experience a fixed rate of mortality,* and essentially proposes that continual “culling” is the primary cause for the in-river mortality experienced through the hydrosystem.

After reviewing the CSS Final Report and materials for this review, the ISAB has two fundamental reasons for not supporting this hypothesis (the CSS Final Report 2004 does not provide supportive evidence for the hypothesis either):

1) The spring/summer Chinook and steelhead under consideration are already 1+ years old and have passed the stage of initial early mortalities in freshwater. The migrants of these Chinook and steelhead are larger fish, and we see no reason to speculate on a fixed

mortality rate in larger migrant fish. It is possible that early migrants of hatchery Chinook and steelhead could have a higher initial mortality after release, but much of this mortality would occur before these fish reached Lower Granite Dam.

2) There is no physiological process known that would result in a fixed mortality rate. Potentially a pathogen, expressed when these fish are under stress (transportation or downstream migration in the hydrosystem), could result in similar mortality rates, but these would not be fixed, nor would they be expected to be fixed each year.

The Data

Estimation of latent mortality of Chinook and steelhead salmon that migrate in-river through the Columbia River hydrosystem involves a maze of statistical models and assumptions, but the data are well defined. The analyses reviewed involve three types of data, but subsets of data may be selected for any specific analysis. The basic data sets include:

1) Stock and recruitment data for index populations of spring/summer Chinook within the Columbia River Basin (seven populations within the Snake River and three within the John Day River). These data date from the 1950s to present but vary between populations. The data relate the number of adult salmon returning ($R_{i,t+n}$ = recruits produced from population i, in spawning year t) to the Columbia River to the number of parental spawners ($S_{i,t}$) that produced them.
2) Passive Integrated Transponder (PIT) tags applied to juvenile spring/summer Chinook and steelhead (hatchery and wild, in-river migrants or barged fish) uniquely identify individual fish. Various portions of the PIT Tag Information System (PTAGIS) database are used in different analyses, but two sets of PIT data are most commonly referred to. These data include the NMFS PIT data for 1995-2002 (Williams et al. 2005, Scheuerell and Zabel *draft ms* (text files: https://secure.bpa.gov/salmonrecovery/), Muir et al 2006); and Comparative Survival Study (CSS) tags for 1994-2004 out-migration from the Snake and John Day rivers (Berggren et al. 2006).
3) Environmental covariates to account for changes in the hydrosystem flow regimes over time, estuary and near-shore marine conditions, and larger scale climate variation. Numerous environmental parameters have been applied by different authors (Berggren et al. 2006, Petrosky et al. 2006, Paulsen and Fisher *in review*) to account for environmental trends and cycles within the time series of stock/recruit data and smolt-adult survival rates.

The various hypotheses presented (described above) can be related based on types of data involved and models applied (Figure 2).

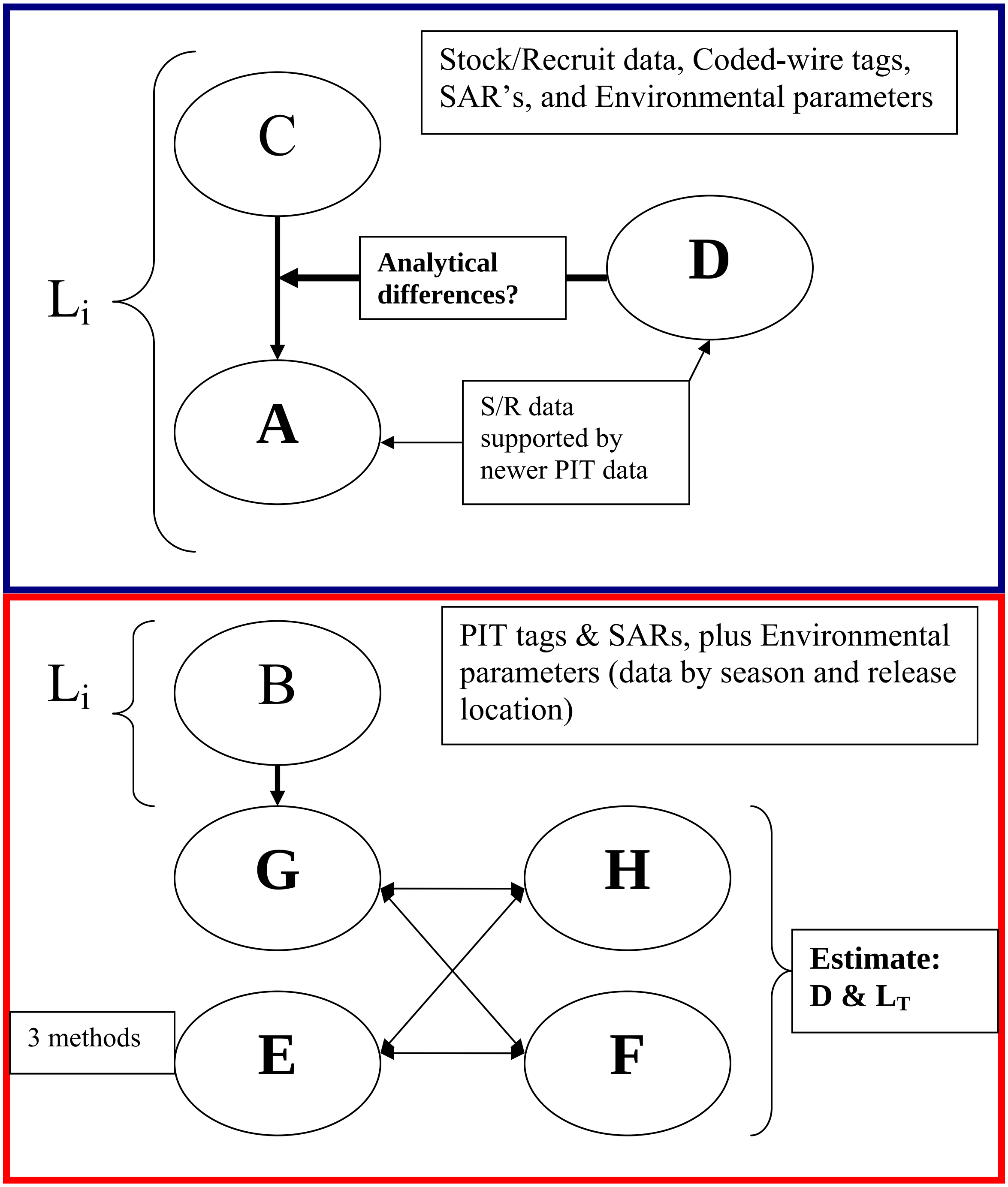

Figure 2. Relationships among hypotheses and supporting data.

Before commenting on the individual data sets, it is worth recognizing the challenge involved in estimating the magnitude of latent or delayed mortality. Since it is defined as the mortality of in-river migrants downstream of Bonneville but attributed to effects of the hydrosystem, delayed mortality cannot be observed and must be estimated **indirectly**. Extensive and creative effort has been focused on how to assess delayed mortality and the relative survival of transported fish versus in-river migrant fish from Bonneville to their return as adults (notably, see Marmorek et al. 2004) (www.fpc.org/documents/CSS/CSSworkshop_reportfinal.pdf).

While some level of delayed mortality likely does occur each year, its value may be highly variable and its magnitude and variability could differ among populations of salmon and years of downstream migration. Until the development of the PIT tags, stock/recruitment analyses were the bases for estimation of latent mortality, but these analyses inherently require a long time-series of information (on production from a known number of spawning adults) and assume random background environmental condition. This condition is seldom true, particularly within the Columbia Basin, due to changes in physical environmental conditions in the Columbia that are the background to any assessment of stock/recruitment for Columbia Basin salmonids. In addition, climate variation must also be super-imposed and, although several authors have appropriately begun to evaluate variation in climate factors to account for annual deviations in stock/recruitment rates, smolt-to-adult survival rates, and estimation of delayed mortality, the pattern of climate effects introduces two issues that also merit consideration:

a) Is the cumulative impact of climate-related factors symmetric with respect to the impact of delayed mortality or do poor conditions have greater impacts?
b) How does the period of climate cycles or trends compare to generation time of the salmon? For example, following a series of poor survivals, would we anticipate the salmon to have sufficient time to recover?

The combination of these issues could have serious consequences for the recovery of a salmon population and for what may be perceived as an “acceptable” level of hydro-related mortality (both direct and in-direct) on a population. For example, in periods of good ocean climate and high productivity, does it matter if delayed mortality was minimal or is the critical issue how extensive mortality becomes during poor environmental conditions? The answer to the latter question will be tied to the expected duration of the environmental regimes, how depressed in abundance the populations became, and our capability to manage mortality factors.

The challenge in assessing delayed mortality involves estimating a value that is likely conditioned by annual climate variation (at various spatial scales) set against physical environmental conditions that also change but at different scales of time and space. Given this situation, any future value of latent mortality will have a high degree of uncertainty.

Stock and Recruitment Data: (see Deriso et al. 2001; Petrosky et al. 2006; Paulsen and Fisher, *in review*; Schaller and Petrosky, *in review*)

Each of the analyses using stock and recruitment data (in this current review) use spawning escapement data for seven “index” populations within the Snake River and three “index” populations in the John Day River. Total returns to the Columbia River are estimated by run reconstruction, accounting for the number of spawners, in-river harvest, and inter-dam losses by age for each population (run reconstruction method described in Beamesderfer at al. 1997). The time series of data varied among populations but was typically broken into two time periods, pre and post the 1970-1974 period of dam completion in the Snake River. Various models account for density-dependence (the number of spawners), time period, and common year effects between populations or environmental covariates (references above). However, the most significant difference between the models presented was the assumption that **all** populations had a common productivity parameter (Snake and John Day populations, Hinrichsen, *pers comm*) as opposed to using separate estimates of productivities for each population or region for the Snake River and the John Day basins. The assumption of a common productivity value had a major impact on the productivity estimated (much lower) and greatly decreased the estimated delayed mortality to near zero. The use of a common productivity parameter between two geographically discrete population groups was strongly refuted in an August 14, 2006, memo from Ron Boyce, Charlie Petrosky, Howard Schaller, Earl Weber, Rod Woodin, and Peter McHugh to Ed Bowles and Chris Toole, Chairmen of the Framework Group.

It may be argued that differences in results due to assuming common versus differing productivities can be explained by trends in environmental variation. Schaller and Petrosky (in press) show that patterns of residuals of Ln(R/S) over time are strongly correlated between the Snake and John Day populations and are not randomly distributed with time. Consequently, patterns in residuals could be explained by examining environmental covariates (Paulsen and Fisher *in review*). If the climate covariates account for the trends, then the stock/recruitment analyses would be expected to better estimate the density-dependent recruitment functional relationships within populations.

Although the discussion concerning interpretation of stock and recruitment analyses, environmental covariates, and the value of upstream (Snake River) versus downstream (John Day River and Carson hatchery) continues (Hinrichsen *pers comm*, Paulsen and Fisher *in review*, Schaller and Petrosky *in review*), the ISAB questions whether this continuing discussion is productive. Compared to the value of PIT-tag information, stock/recruit (S/R) analyses are a blunt instrument for assessment of annual delayed mortality. Numerous authors are now using PIT tag data to support the S/R findings and estimating smolt-to-adult survival rates and/or recruitment at age-3 (survival to Age-3, one year after entry to the marine environment). Regional commitments to increased PIT tag application and detection capabilities in several dams for juveniles and adults, now provide substantial new information on the mortality of individual fish related to seasonality, location, and size at tagging, downstream and upstream passage history, predation risks, and such.

PIT Tag data: (see: Berggren et al. 2006, Marmorek et al. 2004, Muir et al. *draft ms*, Petrosky et al. 2006, Scheuerell and Zabel *draft ms*, Williams et al. 2005, Zabel et al. 2005)

> "The use of passive integrated transponder (PIT)-tag technology in the Snake and Columbia Rivers, with each fish having a unique tag code, has provided an unprecedented opportunity to evaluate survival over the entire life cycle of salmon. PIT-tag detection systems are now installed in the juvenile bypass systems at most mainstem dams and in adult fish ladders of half the dams that Snake River anadromous salmonids pass, allowing evaluation of survival on a much finer scale than allowed by older technologies." (Muir et al. 2006)

The application of PIT tags began in 1987 and in excess of 15 million tags have now been applied to salmonids in the Columbia River Basin. Much of the data and historical information is maintained by staff at the Pacific States Marine Fisheries Commission (PSMFC) in the PIT Tag Information System (PTAGIS database; www.ptagis.org) including data access tools and a very useful library menu linked to documents and peer-reviewed journal publications. The early development of the tagging and detection systems has been described by Prentice et al. (1990a,b) and initial analyses of downstream survival of tagged salmonids reported by Muir et al. (2001) and Williams et al. (2001).

The PIT-tag program is essentially a multiple mark-recapture program with automated detection of tags that eliminates the need to recover and handle tagged animals. The statistical models used in analyses of PIT-tag data have been described by Newman (1997a,b), Skalski (1998), Skalski et al. (1998), Sandford and Smith (2002), and Townsend et al. (2006). As with any mark-recapture program, the information value is limited by the number of tag detections (the “observed” recoveries) and the adequacy of the recovery sampling effort. As electronic detection became more fully developed within the Columbia hydrosystem, detections of downstream migrating smolts (or smolts transported) provided significant information on downstream survival rates, migration timing, and specific-reach mortality, all of which could be related to specific information on individual tagged salmonids. Nevertheless, estimation of smolt-to-adult survival rates could still be limited by the number of adult detections. Ocean survival rates for spring/summer Chinook and steelhead remain only a few percent of the smolts entering the ocean and limit the number of detections possible unless tagging rates and adult up-stream sampling rates can be increased to compensate. This limitation can be compounded by allotting released tags to a variety of release strata defined by seasonal period, stock of origin (tributary, hatchery, etc.), location of release (specific dams), and such.

PIT-tag data greatly increase the number of release strata that can be assessed and opportunities for explanatory studies (e.g., rate of downstream passage, time of entry to the ocean, bird predation rates, size of bypassed smolts, etc.), but the technology can not compensate for the indirect estimation of latent morality. The relatively short time series of PIT tag data also limits ability to relate variation in results to the environmental data applied to the stock/recruitment studies. The same environmental parameters may be considered, but the number of annual comparisons will simply limit comparisons until more annual data are accumulated. The potential value of PIT-tag data though is clearly exemplified by the differences in passage rates, reach survivals, and smolt-to-adult survival measured for downstream migrants in the 2001 drought year (Berggren et al. 2006). The PIT-tag data do continue, however, to support the existence of latent mortality (D values < 1) for Snake River spring/summer Chinook and steelhead, but the value depends on the comparison made (in-river vs. transported, hatchery vs. wild, early vs. later season, etc.) and on environmental conditions during the juvenile emigration year (see Tables B-1 and B-7, Berggren et al. 2006). Two particular points of confusion in the presentation of PIT tag analyses should be noted:

- Given the number of release strata possible with PIT-tag data, it is important for reports to clearly identify the comparisons being made. The interpretation of reports reviewed by the ISAB was complicated by this issue. For example, without full notation of release points, what sources of mortality would be included within a smolt-to-adult survival rate?
- Latent mortality levels can vary with annual environmental conditions, but estimates of “D” (a ratio) may not if the numerator versus denominator responded proportionately to the environmental variation. For example, transported and in-river

> Chinook may both have increased survival rates under favorable marine conditions, but a ratio comparison would be insensitive to such conditions if the two groups responded proportionately. However, a "D" value comparison that includes the in-river survival factor could show greater sensitivity to change in the in-river group due to improved in-river survival that does not affect the transported fish.

Environmental Data: (see: Paulsen and Fisher, *in review*; Petrosky et al. 2006, Schaller and Petrosky, *in review*)

These citations identify the environmental indices applied in recent assessments and will not be reiterated here. The impact (and explanatory value) of environmental conditions will, however, be dependent on the correlations between freshwater, estuary, and marine environmental conditions and parameters. Hinrichsen (2006) provides an example of this point, and some papers reviewed took account of these correlations. In a number of other papers reviewed, though, discussions of outcomes or expected changes in D values show little consideration of this point (beyond recognition now that environmental conditions can have a strong effect on mortality rates).

NOAA's Questions

Finally, we take up the questions posed, attempting to treat alternative models/hypotheses collectively and comparatively for each question. As prelude, we open with a few overarching comments. As has been the case for the downstream passage modules of COMPASS, there are two sets of issues: (1) estimation/testing of competing models of latent mortality, and (2) how to deploy what we learn to seed COMPASS modeling.

Leaving aside estimation/testing for the moment, it remains unclear whether we are after L_I and L_T, SAR_I and SAR_T, TIRs and/or D_{IT}. One thing that is clear is that we are not able to estimate *latent mortality* for the *damless* reference condition. Thus, we cannot estimate the overall, absolute latent mortality associated with the existence of dams. Also, because the background environmental conditions appear to have a major effect on the SARs, we may expect it to take substantial time and effort to measure the relative latent mortality of some operational changes against the background noise of the environment.

There are hypotheses within the set presented to the ISAB that would allow us to address modeling strategies, and most of the hypotheses are (with modification) connectible. They are not mutually exclusive, nor are they exhaustive. Except for hypothesis D, the other hypotheses relate in combination to time or size upon arrival at Bonneville and incorporate seasonal and climatic factors (flows, upwelling, PDO). Evidence shows that an arrival time that is too early or too late can lead to poor survival. Rather than choosing among alternatives, each of which has its own value, our sense is that it would be most profitable to *connect hypotheses* in ways that will allow the COMPASS team to evaluate the interconnectedness of hypotheses and determine relative significance of variables. This would produce a versatile modeling platform for the "below Bonneville" component.

Comments on Questions of Interest

All of these models can be expressed in a common modeling and statistical framework. We note that subsets of the hypotheses group easily into clusters, as portrayed in Figure 2. We will comment on the plausibility and evidentiary support for each of the models below, as requested, but our comments should be viewed less in the vein of promoting a choice of models for the COMPASS modeling team than as an attempt to help them tie things together.

1. Model Plausibility and Data Availability - How plausible is each of the latent mortality hypotheses, based on the evidence presented by the authors (e.g., data, analyses based on those data, and other considerations)? Are the data appropriate for deriving the estimates of interest?

The central point is that the comparative phase of the work lies ahead, guided by a coherent analytical and modeling framework, either that articulated in Figure 2 or by an equally explicit alternative. It is obvious that the simplest (most parsimonious) model is preferable, unless and until compelling evidence indicates the need for a more elaborate specification of the problem.

Hypotheses F and H are minor variants of the same idea, that project-specific variation in TIRs translates into project-specific D_{IT} variation, which later can then be used to model operational alternatives. Hypothesis H adds the wrinkle that the TIRs are also seasonal.

Several models are based on continuously varying river or climatic conditions or on alternative operational strategies, both of which must be modeled in continuous terms. There are three alternative modeling directions, Hypothesis A (water travel time), Hypotheses B and G (seasonality), and Hypotheses F and H (project specificity). These are all somewhat related.

2. Evaluation of Current Hydropower Operation – How applicable is each of the hypotheses for estimating the overall (absolute) latent mortality associated with the existence of dams and current/recent operations? How do the hypotheses rank in this regard? Is sufficient information available for the ISAB to suggest how the hypotheses should be weighted in this type of application?

The question translates as "How well can we determine L_I and/or L_T under operational conditions embedded within recent or projected environmental conditions?" A direct comparison of current *in-river* and *damless* survival rates for the "below Bonneville" component of the life cycle would provide us with an assessment of L_I. As we pointed out, however, we cannot directly observe the *damless* river condition, and that leaves us trying to argue backwards from what we can see to what we cannot. As pointed out by the proponents of Hypothesis D, that is extraordinarily difficult to do: too many other factors are involved, and they are all confounded. Although historical pre/post dam survival comparisons provide us with some information, we note that S/R estimates are not as credible as the PIT tag estimates. Therefore credible estimation of L_I remains elusive.

It seems that both SAR_I and SAR_T are credibly measurable for any given year (on average) and, with less precision and accuracy, for particular seasons, single projects, or under changing circumstances. We can compute the SAR-ratio,

$$D_{IT} = \frac{SAR_{T,\,Bon \to LGR}}{SAR_{I,\,Bon \to LGR}} = \frac{(1 - L_T) \bullet S_{T,\,us}}{(1 - L_I) \bullet S_{I,\,us}}$$

And, assuming that we can separately measure $S_{T,us}$ and $S_{I,us}$ (or can reasonably assume them to be equal), we can establish the ratio $(1 – L_T) \div (1 – L_I)$ thus establish L_T relative to non-measurable L_I.

SAR_I and SAR_T are associated with various predictor variables, some environmental, some operational (not being assessed for this question), and some representing interactions. The array of potential predictors is large and they vary in a mutually dependent complicated fashion. Simple hypotheses are easy to evaluate, while more elaborate hypotheses require ever more information and tighter specification of the connections between the variables. For simple hypotheses, crude data are adequate, but for more elaborate hypotheses, sampling errors or uncertainties can create *faux* signals. The simpler the model the greater our inferential power, while more complex models increase the challenge of the modeling task.

3. Evaluation of Operational Alternatives - How applicable is each hypothesis for estimating *changes* in latent mortality associated with alternative operations? How does each hypothesis rank with respect to providing plausible estimates? Is sufficient information available for the ISAB to suggest how the hypotheses should be weighted in this type of application?

The ISAB does not intend to rank the hypotheses. Rather our review is intended to identify hypotheses that might best inform operational alternatives in the short-term, given the data that are available. We cannot use any hypothesis that sets SAR_I and SAR_T constant for a whole year, for a particular season, or for a particular project, except as null hypothesis (reference) models against which to compare more elaborate models with changes in the operational regime for any one/combination of the separate projects. Models/Hypotheses D and E will be of little help in evaluating operational alternatives. Model C is also not helpful unless we specify separate parameters for each particular set of operational variables, not an attractive modeling option.

For Model A, we should be able to convert altered sets of project operations into changes of WTT for any given week or for a whole season, so it should be possible to assess the impact of changing WTT on the SARs. How well we could assess the impact of changing operations would depend on (a) how well we can translate those operational changes into WTT, (b) the extent to which changing operations impact WTT, and (c) the extent to which WTT predicts the SAR outcome. Similarly, to the extent that we can convert project-specific operational changes into distributions of arrival times at the estuary, it should be possible to use Model B to assess the impact of those operational changes, in a general way. As with Model A, the assessment would have to be indirect, with the same sorts of caveats as for Model A.

Model G shows promise for evaluation of operational changes, since it is couched in terms of specific projects, and because both L_I and L_T are examined. Model F yields project-specific estimates and should be assessable under changing project-specific operations, but it leads to tabular output. While a table may be a convenient source of parameter values to plug into

COMPASS, it is less than ideal for evaluation of a continuum of operational alternatives. On the other hand, if operational changes alter the lognormal parameters, μ and σ, in a simple and continuously predictable way, Model F might be quite interesting in this vein. Model H adds a seasonal element to the project-specific focus and is something of a blend of F and G. It should be possible to keep track of the separate groups taking any particular route from above Lower Granite to below Bonneville and to follow their subsequent survival experience. That will require a multi-state demographic treatment, but a proper accounting through careful design to gather appropriate PIT-tag data is a requisite.

The more indirect the inferential pathway, the greater will be the uncertainty in the inferential outcome. Models G, F, and H are the most empirical, making best use of available data. The ISAB is also aware that NOAA Fisheries (Matthews and Muir 2006) has an ongoing transport/in-river study to evaluate hydropower system-related latent mortality associated with passage of yearling Chinook through the Snake River dams. Within the next several years, if sufficient numbers of adults from the tagged groups return, the results may apply as a test related to latent mortality hypothesis C. Models A and B are not likely to be informative without further elaboration. Models D and E do not appear useful for the analysis of alternative operations.

4. Evaluating Listed Columbia Basin ESUs **–** To what extent are the hypotheses and methods described applicable to ESUs other than Snake River spring/summer Chinook salmon? Is information presented or referenced that permits such inferences? Comment on the 13 listed ESUs for the Columbia River Basin, separately for each listed ESU.

The Framework team points out that the hypotheses described above were developed for Snake River spring/summer Chinook, and in some cases for Snake River steelhead. They request information on Snake River fall Chinook and Snake River sockeye, in particular, and the question has been generalized to include all of the listed ESUs.

Our first comment is that any ESU that is not routinely transported can yield no estimates of SAR_T and therefore no estimates of D_{IT} or L_T. On the other hand, we might profitably be able to compute a SAR-ratio for any pair of competing operational alternatives, as long as we can divide the smolts into separately trackable cohorts. For alternatives A and B, we have

$$D_{AB} = \frac{SAR_{B,\,Bon \rightarrow LGR}}{SAR_{A,\,Bon \rightarrow LGR}} = \frac{(1 - L_B) \bullet S_{B,\,us}}{(1 - L_A) \bullet S_{A,\,us}}$$

We can obtain the ratio $(1 - L_B) \div (1 - L_A)$ and, while we can obtain neither L_A nor L_B in absolute terms, we can certainly obtain the ratio between them, which provides a comparative metric that can be used for evaluation of the impacts of changing operations, variable river, variable climate, or variable ocean situations.

5. Can We Improve the Hypotheses? – Can we suggest modifications to any of the hypotheses and analyses to make them more useful? Would these changes affect the rankings or weightings?

Hypothesis A. Before this relationship can be implemented in COMPASS, the authors have indicated that they will need to confer with COMPASS modelers to ensure that estimates of WTT are equivalent in the regression and the COMPASS model (consider adjustments to WTT based on changes to the Lower Granite to Bonneville fish travel time from probable reductions in forebay delays due to hydro actions) and to determine if any conversion steps are necessary. There will also need to be some discussion regarding how to implement the ocean/climate environmental variables.

Hypothesis D. It seems that since we cannot measure latent mortality in absolute terms, we should not make any assertion as to its magnitude for modeling purposes. The information presented in support of Hypothesis D establishes confounding in estimates of latent mortality but does not establish anything about the size of latent mortality. And it does not support the conclusion that latent mortality is 0 or very near 0.

Hypothesis G. This relationship is already implemented in COMPASS as an average relationship across years. We suggest that the COMPASS group pay particular attention to assumptions underlying estimation of seasonal in-river survival, since only the timing of bypassed in-river migrants is known.

Hypothesis H. To implement in modeling, it would be assumed that future action is either high spill/no transport at LGR or no (voluntary) spill/max transport at LGR during any given week in the season. We suggest that the COMPASS group pay particular attention to assumptions underlying estimation of seasonal in-river survival, since only the timing of bypassed in-river migrants is known.

If we cast hypotheses in a single coherent framework, reflecting the network in Figure 2, we facilitate statistical estimation/testing and subsequent COMPASS modeling. The COMPASS team has shown a penchant for log-linear models of the form shown in the various survival equations used to describe the hypotheses above. Our penchant is for logit-linear models, which are a little more versatile for comparative modeling. We will pose our suggestions in that latter vein. Pending a clearer statement of the problem, it is not clear what the overall purpose of the investigation is. Recall the four alternatives mentioned in our introductory comments. Our sense is that one favored alternative is to measure the SARs and the SAR-ratios, pursuing differential latent mortality for in-river vs. transported smolts. If so, we need a framework that can handle both, and such considerations lead us to the suggestions detailed in the appendix.

Another promising alternative is to combine all hypotheses except Hypotheses C and D (which directly assert the result that latent mortality is large or small). The remaining hypotheses include various components of latent mortality and could be merged into a single, integrated model. A merged data set could then be used to evaluate this model, and the statistical analysis should be able to determine that some of the components are not particularly important and that others are significant when it comes to estimating post-Bonneville mortality (see Catchpole et al., 1998; Fournier et al., 1998; Maunder, 2001; and Goodman, 2004, for examples of merged data sets). This global modeling method of analysis could be used to integrate the investigation of the four alternative approaches discussed in our introductory comments.

6. Future Monitoring and Research – What lines of future research and monitoring would be most valuable for reducing the uncertainty associated with the magnitude of and mechanisms responsible for latent mortality?

The ISAB perspective on the scope and feasibility of research needed to address the latent mortality uncertainties may be framed with a series of questions. What is really knowable, given the limits of our ability to measure behavior and survival in the estuary and ocean and to compare various stocks (genetics, life histories) that pass different dams, at different sizes, at different times? Can we clearly identify causative models or are we necessarily dealing with retrospective phenomenological descriptions? Can we really get useful answers from research on these issues? Under what circumstance do we meet the point of diminishing returns (cost effectiveness) on conducting research?

A looser, weight of the evidence management approach might be needed because of the great variability and the difficulty of measuring the various sources of mortality, as well as the time it will take to fill the remaining information gaps. In the long term, we can better define the noise, but it is still likely that analyses will need to address how to handle the large, unidentified noise in estimates of fish performance. There is a high degree of uncertainty in any estimates based on limited time series. Ocean conditions that affect survival vary greatly on several time/space scales. The ISAB strongly believes that such uncertainty needs to be acknowledged; management must take into account the uncertainty, not just the mean. This implies that the region must manage for the highest risk, i.e., must select management strategies that are robust to the uncertainty.

Identifiable factors that contribute to variability in post-Bonneville mortality may inform future monitoring and research needs. These needs may include biological factors already mentioned:

- Predation by birds, especially Caspian Terns and cormorants
- Predation by pikeminnow and marine fishes (hake)
- Increased vulnerability to predators because of size, stress, or disease
- Timing of ocean entry
- Ocean conditions, including density dependent factors, upwelling, spring transition, ENSO and PDO
- Ocean interceptions and harvest of returning adults
- In-river adult pre-spawn mortalities (harvest, dam passage, marine mammals, disease, high temperatures)

While future research and monitoring may take many years to estimate these various sources of mortality, some new and developing technologies offer the potential to do so. Although PIT tags provide estimates of direct mortality within the hydrosystem down to Bonneville Dam, there are not observations of the PIT tags beyond Bonneville Dam that would allow for estimation of mortality in the lower river and estuary. Currently, lower river and estuary mortality are combined within the total mortality in the marine environments, including coastal and open ocean life phases (noted as $S_{e/o}$). The relatively recent developments of acoustic tag systems have given rise to several studies designed to estimate survival of spring/summer Chinook and steelhead for the lower Columbia River below Bonneville, to and through the estuary, and the

Pacific Ocean shelf (Welch and Rechisky 2007, a joint Kintama Research and UBC study; McComas et al. 2006, a joint NOAA Fisheries and PNL study). The application of acoustic tags in these large smolts would allow for separation of effects by time/area in the lower river, estuary, and plume and near-shore coastal zones (and new information on habitat use, migration rates, etc.). However, a new tag-type introduces new uncertainties about the impact of these larger tags on the survival and migration of emigrating smolts. A continuation of the PIT-tag programs, coupled with an acoustic tagging program would provide for direct comparisons between tags and direct assessment of mortality rates associated with the acoustic tags. Further, the acoustic tags would only provide new information during the lower river (below Bonneville) and early marine phases. At present, given the size of these smolts, available acoustic tags would only have sufficient battery life for a few months (other programmable tags are available but initial investigations should determine duration of use in the estuary and coastal zone).

Continued comparisons of in-river migrants versus transported fish would require acoustic tags being applied in upper river locations, and the ISAB is aware that both the Welch and McComas studies have tagged fish at up-river locations. Tagged fish would then be allocated to in-river migrant and transported groups. We must caution, though, that these studies are either in the early stages or in the demonstration stage. The estimates currently produced are based on very small numbers of tagged fish and are preliminary. It will likely be a number of years before statistically sound estimates are available and are widely accepted.

Conclusions and Recommendations

The ISAB recommends that an investigation of merging the various components of latent mortality into one grand model be conducted. A merged data set could then be used to evaluate this model with the result that the statistical analysis should aid in selecting among hypotheses by determining which latent mortality components are important when it comes to estimating post-Bonneville mortality (see Catchpole et al., 1998; Fournier et al., 1998; Maunder, 2001; and Goodman, 2004, for examples). Hypotheses C and D that directly assert that latent mortality is large or small would not be included in this investigation.

The ISAB also recommends a logit-linear approach (presented in Appendix A) be investigated as a potential alternative approach/framework for future modeling.

There is a high degree of uncertainty in any estimates based on limited time series. Ocean conditions that affect survival vary greatly on several time/space scales. The ISAB strongly believes that the uncertainty needs to be acknowledged and efforts continue to reduce this uncertainty. Future monitoring and research is needed to further quantify biological factors that contribute to variability in estimated post Bonneville mortality. In particular, the ISAB recommends that acoustic tags continue to be developed and used to assess mortality in the lower river (below Bonneville), the estuary, and the Pacific Ocean shelf and to determine how mortality varies in these regions with environmental conditions. As well as acoustic tagging, this will require the continuation of PIT tagging (a monitoring and evaluation program) and many more years of data before this question can be assessed further. Analyses of PIT tag data with incorporation of biological and environmental variables has provided useful new insights and this research should clearly continue to provide a necessary time-series.

The ISAB concludes that some latent mortality occurs to fish that experience the hydrosystem. However, researchers/modelers have made estimates of latent mortality ranging from 0.01 to 64%, and the ISAB recommends against continuing trying to measure latent mortality. Its value relative to a damless reference is not useful; instead, the total mortality of in-river migrants and transported fish is the critical issue in this line of inquiry for recovery of listed salmonids and has the considerable advantage of being directly measurable.

Finally, we note that management must take into account uncertainty in fish performance, not just the mean. This implies that the region must manage for the uncertainty in estimates of performance and its relationships with management actions.

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Appendix A

(a) Rather than using log-linear models of the form

$$\ln(\mathrm{SAR}_{\mathrm{I},j}) = \ln(\mathrm{S}_{\mathrm{I},j}) = \beta_{0\mathrm{I}} + \beta_{1\mathrm{I}} \bullet x_{1\mathrm{j}} + \beta_{2\mathrm{I}} \bullet x_j + \varepsilon_{\mathrm{I},j} \ ,$$

$$\ln(\mathrm{SAR}_{\mathrm{I},j}) = \ln(\mathrm{S}_{\mathrm{T},j}) = \beta_{0\mathrm{T}} + \beta_{1\mathrm{T}} \bullet x_j + \beta_{2\mathrm{T}} \bullet x_j^2 + \varepsilon_{\mathrm{T},j} \ ,$$

we would suggest general usage of log-linear forms such as

$$\ln\left\{\frac{\mathrm{S}_{\mathrm{I},\,j}}{\mathrm{L}_{\mathrm{I},\,j}}\right\} = \beta_{0\mathrm{I}} + \beta_{1\mathrm{I}}\bullet x_{1j} + \beta_{2\mathrm{I}}\bullet x_{2j} + \varepsilon_{\mathrm{I},j} \quad \text{and} \quad \ln\left\{\frac{\mathrm{S}_{\mathrm{T},\,j}}{\mathrm{L}_{\mathrm{T},\,j}}\right\} = \beta_{0\mathrm{T}} + \beta_{1\mathrm{T}}\bullet x_{1j} + \beta_{2\mathrm{T}}\bullet x_{2j} + \varepsilon_{\mathrm{T},j} \ ,$$

etc., ensuring that all of the survival and mortality estimates are properly bounded, for both models used to predict particular SARs and for those used to predict ratios.

(b) When comparing SAR_T with SAR_I, use the log odds ratio Δ_{IT}, rather than D_{IT},

$$\Delta_{\mathrm{IT},\,j} = \ln\left[\frac{\mathrm{S}_{\mathrm{T},\,j}}{\mathrm{L}_{\mathrm{T},\,j}} \div \frac{\mathrm{S}_{\mathrm{I},\,j}}{\mathrm{L}_{\mathrm{I},\,j}}\right] = \ln\left[\frac{\mathrm{S}_{\mathrm{T},\,j}}{\mathrm{L}_{\mathrm{T},\,j}}\right] - \ln\left[\frac{\mathrm{S}_{\mathrm{I},\,j}}{\mathrm{L}_{\mathrm{I},\,j}}\right]$$

$$= (\beta_{0\mathrm{T}} - \beta_{0\mathrm{I}}) + (\beta_{1\mathrm{T}} - \beta_{1\mathrm{I}}) \bullet x_{1j} + (\beta_{2\mathrm{T}} - \beta_{2\mathrm{I}}) \bullet x_{2j} + (\beta_{3\mathrm{T}} - \beta_{3\mathrm{I}}) \bullet x_{3j} + \varepsilon_j$$

$$= \delta_0 + \delta_1 \bullet x_{1j} + \delta_2 \bullet x_{2j} + \delta_3 \bullet x_{3j} + \varepsilon_j$$

If we define similar models for in-river and transported smolts, but with different values for the regression coefficients, we can estimate $\delta_{0\mathrm{T}}$, $\delta_{1\mathrm{T}}$, $\delta_{2\mathrm{T}}$, etc. That is to say, we define the latent mortality parameters in relative terms, the difference between the *transported* and *in-river* values, avoiding the difficulty associated with the absence of a *damless* river reference set. The alternative hypotheses/models can all be cast in this same general framework, which means we can compare them with log-likelihood and AIC criteria.

(c) A modeling strategy would be to add terms to the model until the log-likelihood or AIC criteria tell us we are not accomplishing anything by adding more terms. This modeling strategy will have analogues for Hypothesis E (and variants) as well as models D and C. The idea is to move from the simple to the complex, judiciously. For example, specification of Hypothesis A should take the form (with x_1 as WTT),

$$\Delta_{\mathrm{IT},j} = \delta_0 + \delta_1 \bullet x_{1j} + (\text{oceanic factors}) + \varepsilon_j \ ,$$

and similarly for Hypothesis B (with arrival time as x_1). We elaborate Hypothesis B as Hypothesis G, for which the following comment might be helpful to the Modeling team. The model for in-river smolts is of the form

$$\text{Logit}\,(SAR_{I,ij}) = \alpha_{I,i} + \beta_{0I} + \beta_{1I} \bullet x_{ij} + \beta_{2I} \bullet (x_{ij})^2 + \varepsilon_{ij} \quad ,$$

as in Hypothesis B, and

$$\text{Logit}\,(SAR_{T,ikj}) = \alpha_{T,i} + \lambda_{T,k} + \beta_{0T} + \beta_{1T} \bullet x_{ij} + \beta_{2T} \bullet (x_{ij})^2 + (\text{day} \bullet \text{site})\text{ interaction} + \varepsilon_{ikj} \;,$$

The interaction term for arrival day and site is probably telling us that β_1 and β_2 vary among sites. A more natural way to model Δ_{IT} would be the following specification

$$\Delta_{IT,ikj} = \alpha_{ik} + [\, \delta_{0,k} + \delta_{1,k} \bullet x_{ikj} + \delta_{2,k} \bullet (x_{ikj})^2 \,] + \varepsilon_{ikj} \;,$$

where α_{ik} is the difference between in-river and transported β_0-values for the j^{th} and k^{th} project. All parameters are now indexed for the particular site of transportation ($k = 1$ for LGR, $k = 2$ for LGS, $k = 3$ for LMN, and $k = 4$ for MCN). We have a separate equation for each transport source, an explicit comparison with the in-river cohort for that year. We thus have a quartet of (arrival-day) logit-quadratic models, correlated across projects, with enough parameters to provide a data-model match that is at least as good as the higher order equation reported by Scheuerell and Zabel (2006), and more straightforward to interpret.