Reply to Zabel and Williams' comments on "Contrasting patterns of productivity and survival rates for stream-type chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers" by Schaller et al. (1999)

Howard A Schaller, Charles E. Petrosky, and Olaf P. Langness

Introduction

In Schaller et al. (1999), we tested hypotheses about spatial and temporal patterns of productivity and survival rates for stream-type chinook salmon (*Oncorhynchus tshawytscha*) in relation to development and operation of the Federal Columbia River Power System. We discussed evidence that supported using these patterns to conclude that the dams had a major effect on the differential decline of upriver stocks. We found little evidence that hatchery, spawning, and rearing habitat or harvest factors could explain the spatial and temporal patterns of stock performance. The comments by Zabel and Williams (2000) do not alter our conclusions.

Zabel and Williams argue that there were three shortcomings of the Schaller et al. (1999) analyses, severe enough to greatly weaken the conclusion that differences in productivity between upper and lower river stocks are primarily due to the number of dams that each must pass. Zabel and Williams first question the premise that the overriding difference between upper and lower river stocks is the number of dams that they must pass, suggesting that different genetic background may predispose the upper stocks to different behaviors and greater vulnerability to environmental conditions independent of the hydrosystem. Second, Zabel and Williams take issue with our analysis of pattern of decline for the upper Columbia River stocks, which they assert did not decline until well after hydrosystem development. Their third point is that missing age composition data might bias the analysis. We address these three alleged shortcomings, and other misstatements about our conclusions, in the following sections.

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H.A Schaller.[1] U.S. Fish and Wildlife Service, 9317 NE Highway 99, Suite I, Vancouver, WA 98665, U.S.A.
C.E. Petrosky. Idaho Department of Fish and Game, 600 S. Walnut Avenue, P.O. Box 25, Boise, ID 83707, U.S.A.
O.P. Langness. Washington Department of Fish and Wildlife, 2108 Grand Boulevard, Vancouver, WA 98661, U.S.A.

[1]Author to whom all correspondence should be addressed. e-mail: howard_schaller@fws.gov

Number of dams

Zabel and Williams question "the premise that the overriding difference between upper and lower river stocks is the number of that dams they pass." Schaller et al. (1999) did not claim that just the number of dams is the overriding factor. We specifically said that it was the effects of increasing hydropower development and operation that appeared to be extremely important in the decline and near extirpation of stream-type chinook salmon stocks of the upper Columbia and Snake rivers. We specifically said that the stocks from the three regions experienced different juvenile migration conditions due to mainstem hydropower development and operations. We further explained that effects included the direct effect of dams, decreased water velocity and increased migration time due to increased impoundment, and increased collection and transportation of juveniles (for the Snake River stocks) to circumvent mortality of juveniles. We explicitly said that we see little evidence of a systematic stressor that selected against upriver stocks, coincident with the declines and unrelated to the hydropower system. The count of number of dams oversimplifies the potential impact of hydropower development and operation. As an example, development of Canadian storage projects in the upper Columbia River in the mid-1970s and hydrosystem regulation has reduced flow during the smolt outmigration (Raymond 1988). This hydrosystem change would have begun to specifically affect upper Columbia River stream-type chinook salmon stocks in the mid-1970s. In addition, the number of turbine units that upper Columbia River stocks could encounter increased by as much as 43 units between 1965 and 1980 (Raymond 1988). Given that our hypothesis involved not just the number of dams, but effects of number of dams and operations, this claimed assumption would not weaken the conclusions of the paper.

Genetic differences

Zabel and Williams imply that there is a "weakness in the assumption that different ESUs [evolutionarily significant units] should respond identically to environmental change." Zabel and Williams hypothesize that genetic difference, and longer migration distances for upriver stocks, could explain

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the differential declines in stock performance. Zabel and Williams state that because these stocks were placed in different ESUs, one would expect upper and lower river stocks to respond differently to changing environmental conditions but provide no empirical evidence to support strong phenotypic differences among the ESUs. The technical document used for the ESU designation (Matthews and Waples 1991) was based primarily on genetic distance values computed for 21 polymorphic gene loci. Matthews and Waples (1991) showed that the estimated genetic distances of upstream and downstream stocks are small (and overlap in some cases). Myers et al. (1998) concluded that Snake River populations show a modest genetic difference in comparison with Columbia River stream-type populations. A minority of the Biological Review Team (for the Myers et al. 1998 report) felt that the ESU should be combined with the stream-type spring-run chinook salmon from the Columbia River.

The Schaller et al. (1999) hypothesis tests examined whether productivity and survival rate declined more and became more variable for upriver stocks, which were most affected by hydropower development, than for downriver stocks. The analysis did not assume that "different ESUs should respond identically to environmental change." The relevant issue is not whether there are any genetic differences between stock groupings, but whether genetic differences manifest themselves in a systematic change in stock performance coincident with and unrelated to hydrosystem development and operation. We presented evidence that the stock groupings had similar life history characteristics and behavior, and shared common environments, particularly during a critical period in the estuary and early ocean. We saw little evidence of a systematic stressor from climate influences or hatchery, spawning, and rearing habitat or harvest factors that could explain the observed spatial and temporal patterns.

To evaluate the claim that "longer upstream migrations alone would suggest a greater vulnerability to environmental fluctuations," we examined the long time series (1939–1990) of survival rate indices of the aggregate upriver spring chinook salmon run (Schaller et al. 1999). Patterns of the Pacific Decadal Oscillation and salmon production would indicate that poor ocean and climate conditions existed for Columbia River salmon before the late 1940s and after the late 1970s (Hare et al. 1999). Productivity and survival rates of the aggregate upriver spring chinook salmon run, which is heavily weighted by longer migrating Snake and upper Columbia River stocks, were relatively stable from 1939 until the era of major hydropower development when major declines began (fig. 7 in Schaller et al. 1999). If the populations had exhibited drops in survival rates of similar magnitude early in this time series, one could hypothesize that longer migration distances for upriver stocks in combination with the patterns of oceanic/climatic conditions may have systematically depressed upriver stocks coincident with, and unrelated to, development of the hydropower system. We believe that the evidence from the aggregate run does not support the theory that longer migration distances for upriver stocks could explain the differential declines in stock performance.

Schaller et al. (1999) reported evidence from the literature that common environmental processes influence survival rates of widely separated stocks within broad regions, particularly during the year of ocean entry. Common stock performance patterns were observed for Fraser River stream-type chinook salmon (Bradford 1994), Fraser River sockeye salmon (*Oncorhynchus nerka*), Bristol Bay sockeye salmon (Peterman et al. 1998), and these index stocks of Columbia River Basin stream-type chinook salmon (Deriso et al. 1996). In addition, climate patterns over the North Pacific Ocean may play an important role in determining abundance of different species of salmon originating over a wide geographic range (Beamish and Bouillon 1993).

Ocean recovery rates

Zabel and Williams state that the "same coded-wire tag data referred to by Schaller et al. (1999) provide evidence that upper river and lower river stocks behave differently in the ocean, contrary to the assertions of the authors." Zabel and Williams missed the major point that year-class strength appears to be strongly determined by the estuary and early ocean environments, where upriver and downriver stocks overlap in time and space. The sparse recovery data indicate general overlap of range from California to Alaska fisheries (Schaller et al. 1999). Even if later ocean distribution differs between stock groupings, which is not demonstrated clearly, the primary effect on survival rates would be expected earlier in the life cycle.

The coded-wire tag (CWT) data extracted by Zabel and Williams were not documented but clearly differed from data used in the Plan for Analyzing and Testing Hypotheses (PATH) that we referred to in Schaller et al. (1999). It is unclear which populations were sampled by Zabel and Williams and whether experimental and (or) production groups were included. For example, Zabel and Williams' data set had only 11 expanded recoveries for lower river stocks compared with 94 (41 observed) in the PATH data set.

Their conclusion about behavioral differences is particularly disturbing when one realizes that the recovery proportion differences are at the sixth decimal place. Even if one accepts the Zabel and Williams approach, it is consistent with our findings that all the stream-type chinook salmon harvest rates are less than 1%. This is in stark contrast with ocean-type chinook salmon, which experience harvest rates in the range of 30–40% (PSC-CTC 1988; Peters et al. 1999). Use of pooled release data, and expanded recoveries across years, may also be inappropriate when attempting to make inferences about behavioral changes in population distribution, since brood year strength could mask behavioral change.

The CWT data clearly indicate extremely low rates of ocean recovery for both groups. Inferences beyond this conclusion, such as differences in oceanic migration patterns, may not be warranted given the scarcity of data. The appropriateness of the two-sample proportion test used by Zabel and Williams for the CWT recovery rates is questionable. In fact, de Libero (1986) found, when evaluating aggregate CWT recovery data, that five or fewer *observed* recoveries are probably insufficient for stable estimates. Also, these data are predominated by zero mark recoveries in the ocean recovery strata. Therefore, a large sampling expansion factor applied to a single mark recovery could unduly influence the difference in ocean recovery rates between stock groups.

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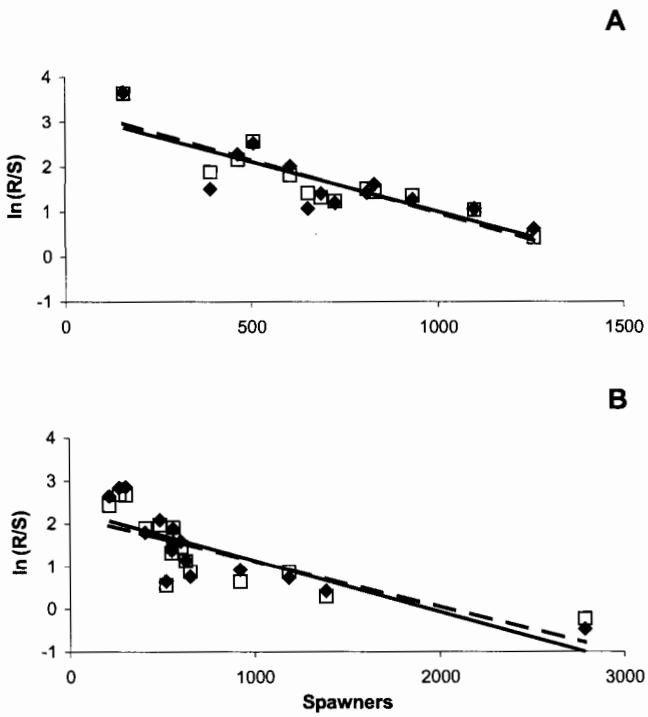
Fig. 1. Sensitivity to the effect of assuming a constant age structure on calculating recruits for pre-1970 return years for two of the Snake River index chinook salmon stocks: (A) Marsh Creek and (B) Minam River. The ln(*R*/*S*) is represented by symbols (diamonds, observed age; squares, constant age assumption) and the linear relationship of ln(*R*/*S*) to *S* is represented by lines (solid line, observed age; broken line, constant age assumption).



de Libero (1986) estimated that it takes between 40 and 50 observed recoveries to achieve a coefficient of variation of 20%. The expanded recoveries of 11, for the lower Columbia River group reported by Zabel and Williams, would represent four to five observed recoveries (applying the average expansion rate that we observed for this group in the PATH data set). According to de Libero's (1986) work, an observed tag number less than five would yield a coefficient of variation of greater than 70% and is probably insufficient for a stable estimate. Given the unstable nature of this estimate, and that the estimated differences in recovery rates are in the sixth decimal place, it appears presumptuous to conclude that this is empirical evidence "that upper river and lower river stocks behave differently in the ocean." Zabel and Williams further hypothesize that this unsubstantiated "behavioral difference" is due to genetic categorization of the upriver and downriver ESUs.

Longer life span

The majority of Snake River fish return as age-5 fish, while lower river stocks primarily return as age-4 fish. Zabel and Williams assert that given differential ocean recovery rates (both substantially less than 1%), this longer ocean residence could easily impact Snake River stocks more than lower river stocks and produce the observed contrasts in recruits per spawner. This conclusion is unsubstantiated and is not supported by the data. Presumably, a poor ocean environment would be especially influential on longer-lived stocks. There are two flaws in this conclusion. First, ocean survival rate patterns appear to be more strongly influenced in the first critical months in the estuary and early ocean environments (where the overlap is greatest between stock groupings; Pearcy 1992; Fryer and Schwartzberg 1993). Second, the adult age composition of the Minam River (in the Snake River) spring chinook salmon stock is younger and more similar to that of lower river stocks, yet the Minam River's stock decline was like that of other Snake River stocks (table 2 in Schaller et al. 1996).

Year of decline

Zabel and Williams argue that "a careful inspection of the mean of log recruits per spawner (an index of survival) by region ([their] Fig. 1) shows that data from upper Columbia River stocks do not support" that declines coincided with upper Columbia River hydrosystem completion in 1968. The log of recruits per spawner, ln(*R*/*S*), for those stocks did not begin to decline until brood year 1975. The hydropower system effects include more than just the number of dams. Effects include increased reservoir storage, reduced water velocity, delayed migration, and number of turbines encountered, all of which continued to change after 1968 (see Number of dams section). Zabel and Williams' reliance on ln(*R*/*S*) is problematic because they ignored density dependence. Recruits per spawner would tend to increase as spawners decrease, and the recruitment functions for the index stocks showed evidence of density dependence (table 2 in Schaller et al. 1999). The appropriate metric would be the deviations from the recruitment relationship (Peterman 1981; Hilborn and Walters 1992), which we termed survival rate indices (SRI-1 and SRI-2). Examination of the patterns of survival rate indices (fig. 5 in Schaller et al. 1999) does not clearly support Zabel and Williams' hypothesized lag in response. Survival rate indices suggest that the decline began between the mid-1960s and the mid-1970s for upper Columbia River stocks; noise in the data prohibits a precise determination of the first year of decline. The general pattern of decline for upper Columbia River stocks appears to be consistent with the observation that hydrosystem effects were in transition after the last dam was constructed (where flows decreased with increasing storage and number of turbines increased).

Age structure bias

Zabel and Williams express concern that lack of age data for lower and upper Columbia River stocks prior to 1970 may "strongly bias" results in the recruitment analysis. The net effect would be to overestimate density dependence (see above section) and productivity (Ricker *a* value). They state that statistical analysis of the effect of period and between regions is "inherently flawed," although limitations "may not change the overall conclusions of the analysis." We find it interesting that Zabel and Williams simultaneously question data quality and present arguments about specific years of decline for regional stock groupings. Although not discussed in Schaller et al. (1999), the missing age structure issue was addressed in a number of sensitivity analyses in the PATH process. PATH sensitivity analyses indicated that the recruit-

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ment functions, and simulated population performance, were relatively insensitive to these age structure assumptions (Deriso 1997).

We investigated the effect of assuming a constant age structure on calculating recruits for pre-1970 return years for two of the Snake River index stocks (Marsh Creek and Minam River), for which we had complete age structure estimates. We estimated the effect of this assumption on the Ricker *a* using the log transformation of our eq. 1 (Schaller et al. 1999) for the pre-1970 period. The effect on the Ricker *a* was small for both stocks (Fig. 1). The constant age structure assumption increased the Ricker *a* by 4% for Marsh Creek and decreased the Ricker *a* by 6% for the Minam River. These were very small changes compared with the total decrease in productivity observed between the pre-1970 and post-1974 periods (table 2 in Schaller et al. 1999). The overall conclusions of Schaller et al. (1999) appear to be robust to the age structure assumptions.

Conclusions

Zabel and Williams assert that problems with (*i*) experimental design, (*ii*) shortcomings in the data used, and (*iii*) weakness in the assumption that different ESUs should respond identically to environmental challenge do not allow Schaller et al. (1999) to rule out other factors contributing to the decline of these stocks. We believe that their assertion about the problem with experimental design is associated with comparing upriver and downriver population performance. This seems to be similar to their third argument that we should not assume an identical response by the different ESUs to a common set of environmental changes. Again, we did not assume that different ESUs should respond identically to environmental change. The relevant issue is not whether there are any genetic differences between stock groupings, but whether genetic differences manifest themselves in a systematic change in performance coincident with and unrelated to hydrosystem development and operation. The empirical evidence supporting behavioral differences in the ocean between upriver and downriver stocks (which are hypothesized to be from genetic differences) is extremely weak. If we assumed that genetic differences do cause a differential response to hydrosystem development and operation, we would still expect the response to be in a similar direction. Indeed, all Snake River anadromous salmonids have been listed under the Endangered Species Act or declared extinct (coho salmon (*Oncorhynchus kisutch*)) since completion of the hydropower system.

The assertion about shortcomings in data appears to revolve around missing age structure. We investigated the claim that bias due to a constant age structure assumption could invalidate our conclusions. Our sensitivity analysis showed that the effect of this assumption on the Ricker *a* was small, consistent with previous investigations in PATH. This finding provides evidence that the overall conclusions of Schaller et al. (1999) are robust to age structure assumptions. Zabel and Williams' final concern is that an overly simplistic interpretation of the data will lead to neglect of other important factors, such as overfishing, habitat degradation, hatchery fish – wild fish interactions, and increases in exotic predators.

We agree with Zabel and Williams that these other factors should not be neglected. Our approach was presented as a first step in a comprehensive decision analysis process. The coincidence in space and time of anthropogenic and environmental factors with the trend in spawner–recruit patterns lends credence to hypothetical assumptions about the importance of those factors in the decline of fish populations. The interpretations that we made were specific to stream-type chinook salmon of the Columbia and Snake rivers. Factors of decline might have different significance for other specific populations (for example, over harvest might be an important factor coincident with the decline of ocean-type chinook salmon from the Snake River). Our paper also emphasized the importance of assessing recovery actions in terms of smolt-to-adult and adult-to-adult survival rates.

We believe that the evidence that we presented and our reply to Zabel and Williams' comments show that we did not oversimplify interpretations of the data, which would "lead to the neglect of other important factors." We conclude that Zabel and Williams' comments do not warrant altering our conclusions in Schaller et al. (1999).

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