Design and Analysis of Salmonid Tagging Studies in the Columbia Basin, Volume IV

Preliminary Assessment of the Effects of Pulsed Flows on Smolt Migratory Behavior

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Preliminary Assessment of the Effects of Pulsed Flows on Smolt Migratory Behavior

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1. INTRODUCTION

The influence of flow on smolt migration behavior has been suspected for a long time. Based upon this belief, there has been a renewed interest in controlling flow, in particular, its pulsating characteristics, to improve smolt migration. Zabel (1994) showed how average flow conditions during individual and cohort downstream migration can improve estimates of migration rates for simple two-parameter travel and time models based on advection-diffusion equations.

While existence of some kind of relationship between flow and some characteristics of smolt migration, such as its speed, is a tempting and intuitive idea with clear management applications, very little evidence exists for a direct effect of pulsed flows on migration speed. Moreover, there is no agreement on how to describe the pulsatile nature of flow.

In the present report, PIT-tag data were used to assess the relationship between flow and smolt-migration speed. Emphasis was placed in the identification of potential predictor variables that could capture the pulsating nature of river flow. The relationship between these pulse variables and smolt travel speed was then investigated. Only river conditions and smolt tagging data from 1994 were used in this preliminary investigation. The intent was to extend these analyses to subsequent years of data. However, the initial findings resulted in equivocating and numerous definitions for pulse and little evidence for relationships with travel speed.

2. MATERIALS AND METHODS

2.1 Data

For this preliminary analysis, we utilized PIT-tag spring and summer chinook that were released upstream Lower Granite Dam during 1994. The original data consisted of the PIT-tag code for each fish and the dates of first and last detection at Lower Granite (**LGR**), Little Goose

(**LGS**), Lower Monumental (**LMN**), and McNary (**MCN**) Dams. Initially, individuals were separated into 2 sets according to their rearing types (**H** = hatchery and **W** = wild). Traveling times for each fish through the three reaches (LGR-LGS, 60 km; LGS-LMN, 40 km; LMN-MCN, 119 km) were calculated as the difference between the last detection date recorded at each dam (LGR, LGS and LMN), hereinafter referred to as release date, and the first detection at the subsequent downstream site (LGS, LMN and MCN), subsequently called arrival date. In this way, the original data produced three subsets of traveling times that were transformed into individual fish speeds by dividing the distance of the reaches by the individual travel times (Fig. 1). Flow data for LGR, LGS and LMN Dams were obtained from the Columbia River Data Access in Real Time (DART) database.

The six subsets of individual fish speeds had different sample sizes ranging from 374 to 1014 fish (Table 1). Moreover, these speeds corresponded to fish that left LGR, LGS, or LMN at different release dates. To account for these differences, we focus our analysis on average speeds of fish groups instead of on individual fish speeds. Fish groups were defined based upon release dates. Table 1 shows the sample sizes for each of these groups. Notice that although there were many individual speeds in each subset, the number of groups was fairly small (40 to 57). Moreover, many of these groups have very small sample sizes. Only the last weeks of April, and May were intensely sampled, and available for analysis.

2.2 Response Variable

The response variable was the harmonic mean speed for the fish groups (*HS*), defined as:

$$HS_j = \frac{n_j}{\sum_{i=1}^{n_j} \frac{1}{S_{ij}}},$$

Figure 1: Relative frequency distributions of individual fish speeds (km/day) by reach and fish type (W = wild chinook, H = hatchery chinook).

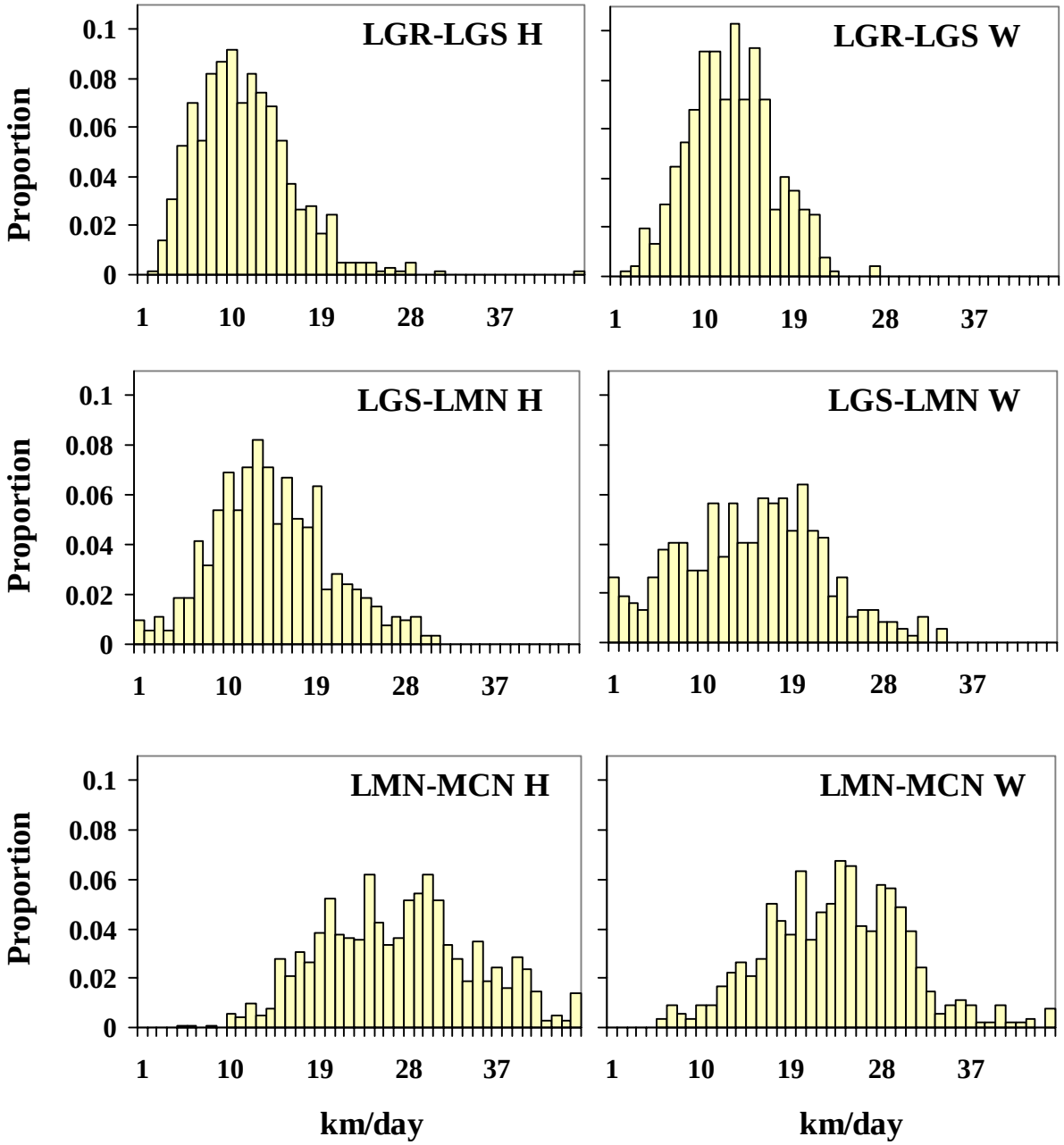


Table 1: PIT-tagged wild (W) and hatchery (H) chinook leaving LGR, LGS and LMN dams that were subsequently detected at LGS, LMN and MCN dams, grouped by release date (month, day, 1994) and reach.

Mo.	Day	LGR-LGS H	LGR-LGS W	LGS-LMN H	LGS-LMN W	LMN-MCN H	LMN-MCN W
4	15						
4	16		1				
4	17		1				
4	18		1				
4	19	1	1				
4	20	7	11				
4	21	30	32				
4	22	46	38				
4	23	32	54	2	2		
4	24	63	39	17	14		
4	25	56	34	23	26	1	3
4	26	37	23	24	27	4	8
4	27	15	16	45	30	5	8
4	28	20	22	29	20	47	42
4	29	11	15	31	23	18	13
4	30	16	24	41	23	46	26
5	1	22	11	20	16	35	33
5	2	9	13	29	14	22	21
5	3	14	4	21	16	23	11
5	4	8	13	17	9	31	27
5	5	10	5	17	13	82	46
5	6	19	9	25	6	52	32
5	7	16	15	9	4	37	25
5	8	29	8	11	10	42	21
5	9	26	12	11	8	56	25
5	10	33	15	3	5	51	14
5	11	31	8	10	6	44	27
5	12	9	10	16	5	42	15
5	13	12	5	10	3	32	12
5	14	15	4	17	6	36	11
5	15	7	10	20	2	62	6
5	16	12	8	17	8	26	14

Table 1 (continued)

Mo.	Day	LGR-LGS H	LGR-LGS W	LGS-LMN H	LGS-LMN W	LMN-MCN H	LMN-MCN W
5	17	4	8	16	8	30	9
5	18	3	4	9	6	46	9
5	19	2	7	7	7	44	11
5	20	7	1	5	4	17	15
5	21	8	2	3	3	31	12
5	22	2	1	3	4	8	1
5	23	2	1	1	2	1	3
5	24	1	3	4	1	2	2
5	25	1	1	1		3	3
5	26	2	1	2	1		
5	27		1	6	5	6	
5	28			4	6	6	1
5	29	3	2	3	3	6	2
5	30	2	4	1	1	4	6
5	31		1	1		3	2
6	1					4	
6	2				1	3	1
6	3						1
6	4			1	1		2
6	5				3	1	2
6	6						
6	7				1		2
6	8					1	
6	9				1		1
6	10				1		
6	11						1
6	12						
6	13						
6	14						
6	15			1	1		
6	16		3				
6	17		1		3		1
6	18				3		3
6	19		1				

Table 1 (continued)

Mo.	Day	LGR-LGS H	LGR-LGS W	LGS-LMN H	LGS-LMN W	LMN-MCN H	LMN-MCN W
6	20				1		
6	21						
6	22				1	1	
6	23		1				1
6	24						
6	25						
6	26						
6	27						
6	28						
6	29						
6	30						
7	1						1
7	2						
7	3			1			
7	4						
7	5		1				
7	6						1
7	7						
7	8	1	1			2	
7	9				1	1	1
7	10		1		2		1
7	11		1				
7	12						
7	13		1		1		
7	14		1				
7	15		1				
7	16				1		
7	17		2		2		
7	18				1		
7	19						
7	20				1		
7	21						
7	31				1		
N		644	514	534	374	1014	535
Groups		41	57	42	56	43	49

where $S_{ij} = \frac{d}{TT_{ij}}$ is the speed of fish *i* released date *j*. TT_{ij} is the travel time (in days), *d* is the distance between the two dams (in km), and n_j is the numbers of fish released on day *j*.

The use of harmonic means instead of arithmetic means was deemed appropriate, given that the data are rates (Zar 1984, p. 24; Freund and Simon 1992, p. 48). For example, if a fish made an average speed of 10 km/day through the 40 km separating LGS and LMN, and another fish that left LGS the same day kept a much faster speed of 40 km/day, the average speed for this group of two fish is the harmonic mean, 16 km/day, not its arithmetic mean, 25 km/day. Since the travel times for the two fish were 4 and 1 days, for the slow and fast fish, respectively, the mean average travel time for the group is 2.5 days. If we divide the distance traveled by the arithmetic mean speed, we obtain an average travel time of 1.6 days (i.e., 40/25 = 1.6). Only if we use the harmonic mean, the right average travel time for the group is obtained (i.e., 40/16 = 2.5).

2.3 Predictor Variables

A series of predictor variables were used in the analysis. Each of them attempts to describe some characteristic of the pulsed flows. A brief description of these variables and their expected relationships with migration speed follows.

2.3.1 Flow on release day *j* (*F*)

This variable was introduced to assess a direct effect of flow on the migration speed of fish on a daily basis. It was expected that groups of fish released on days of high flows would present larger average speeds through the reach.

2.3.2 Average of mean daily flows (*MF*)

Because fish belonging to a particular group based upon release date would have being exposed not only to the flow conditions of the release day but also to those of subsequent days, the average flows at release site during travel time was calculated for each fish of a release group, and these were subsequently averaged for each group. Thus, *MF* for fish group *j* was expressed as

$$MF = \sum_{i=1}^{n_j} \overline{F}_{i,j} \Big/ n_j$$

where

$$\overline{F}_{i,j} = \sum_{t=1}^{TT_{i,j}} F_{t,i,j} \Big/ TT_{i,j}$$

and $F_{t,i,j}$ is the flow at release site experienced by fish *i* of release group *j* on day *t*, n_j is the total number of fish in release group *j*, and $TT_{i,j}$ are the number of days that fish *i* of group *j* spent traveling between the release and arrival damns of a particular reach. It was expected that *MF* would also have a positive relationship with the average speed of a fish group.

2.3.3 Average of variances of daily flows (*FVAR*)

It was expected that not only the average flow conditions encounter by the fish of a particular release group might affect its average speed, but also the day-to-day variations in flow during travel time could also influence the average speed of the group. Whether this influence should be positive or negative was not obvious. *FVAR* was expressed as:

$$FVAR = \sum_{i=1}^{n_j} VAR(F)_{i,j} \Big/ n_j$$

where

$$VAR(F)_{i,j} = \sum_{t=1}^{TT_{i,j}} \left(F_{t,i,j} - \overline{F}_{i,j}\right)^2 \Big/ \left(TT_{i,j} - 1\right).$$

2.3.4 Average flow change (*Fch*)

We defined flow change as the difference in flow between release and arrival days, measured at the release dam. Thus average flow change (*Fch*) is expressed as

$$Fch = \sum_{i=1}^{n_j} \Delta(F)_{i,j} \Big/ n_j$$

where $\Delta(F)_{i,j} = F_{T_r,i,j} - F_{T_a,i,j}$, and $F_{T_r,i,j}$ is the flow at release site experienced by fish *i* of release group *j* on release day T_r and $F_{T_a,i,j}$ is the flow at release site on arrival day T_a for the same fish. As in the case of the previous variable *FVAR*, this predictor variable was expected to capture part of the variability in flow conditions encountered by the fish of a release group during their travel times. In this case, too, the type of influence on the average speed of the group was not clear. Large *Fch* may either increase or decrease average speed.

2.3.5 Orthogonal contrast of flow (*P*)

Daily flows can be transformed into a new variable by means of orthogonal contrasts. This new variable P_j evaluates the flow at the release site on release day *j* (F_j) with respect to the daily measures of flow over an odd number of *k* consecutive days. If flow presents a linear trend

during the k days, P_j will be zero (Fig. 2*a*). On the other hand, when there is a spike in flows, P_j will take a positive value (Fig. 2*b*), and when flows drop, P_j will be negative (Fig. 2*c*).

For the present analysis, we considered periods of length k = 3 and 5 days. For these two period lengths, P_j was defined in two different ways, according to the order the release day had in the series of k days. Thus, when release day j was the first day in the series the predictor variables, hereinafter termed *P3* and *P5*, took the forms:

$$P3_j = -1F_j + 2F_{j+1} - 1F_{j+2}, \text{ for } k = 3 \text{ days, and}$$

$$P5_j = -2F_j + 1F_{j+1} + 2F_{j+2} + 1F_{j+3} - 2F_{j+4}, \text{ for } k = 5 \text{ days.}$$

When release day j was the center of the series k days, the predictor variables *P3c* and *P5c*, took the forms:

$$P3c_j = -1F_{j-1} + 2F_j - 1F_{j+1} \text{ and}$$

$$P5c_j = -2F_{j-2} + 1F_{j-1} + 2F_j + 1F_{j+1} - 2F_{j+2},$$

for k = 3 days and k = 5 days, respectively. As examples, Figure 3 contrasts the flow, *P5c* and *P5* time series at LGR in 1994, and Figure 4 shows the time series of *P3c* and *P3*.

2.3.6 Coefficients of linear regressions between flow and day

The general linear trend of flow change on release day can be described by simple regression lines over short periods of time. For example, the nine hatchery fish that were released at LGR on May 12, 1994 (Table 1) will be represented by the sequence of flows F_j, where $j = 0,1, 2,.., k$ days after release, and $j = 0$ corresponds to May 12. The regression line between F_j and j will describe the general linear trend of flow over a period of $k + 1$ days. The intercept of this regression represents the expected flow at release day ($j = 0$) in the case of a linear relation

Figure 2: Examples of orthogonal contrasts calculated for different patterns of flow (***a***) linear trend, (***b***) spike in flows, (***c***) drop in flows.

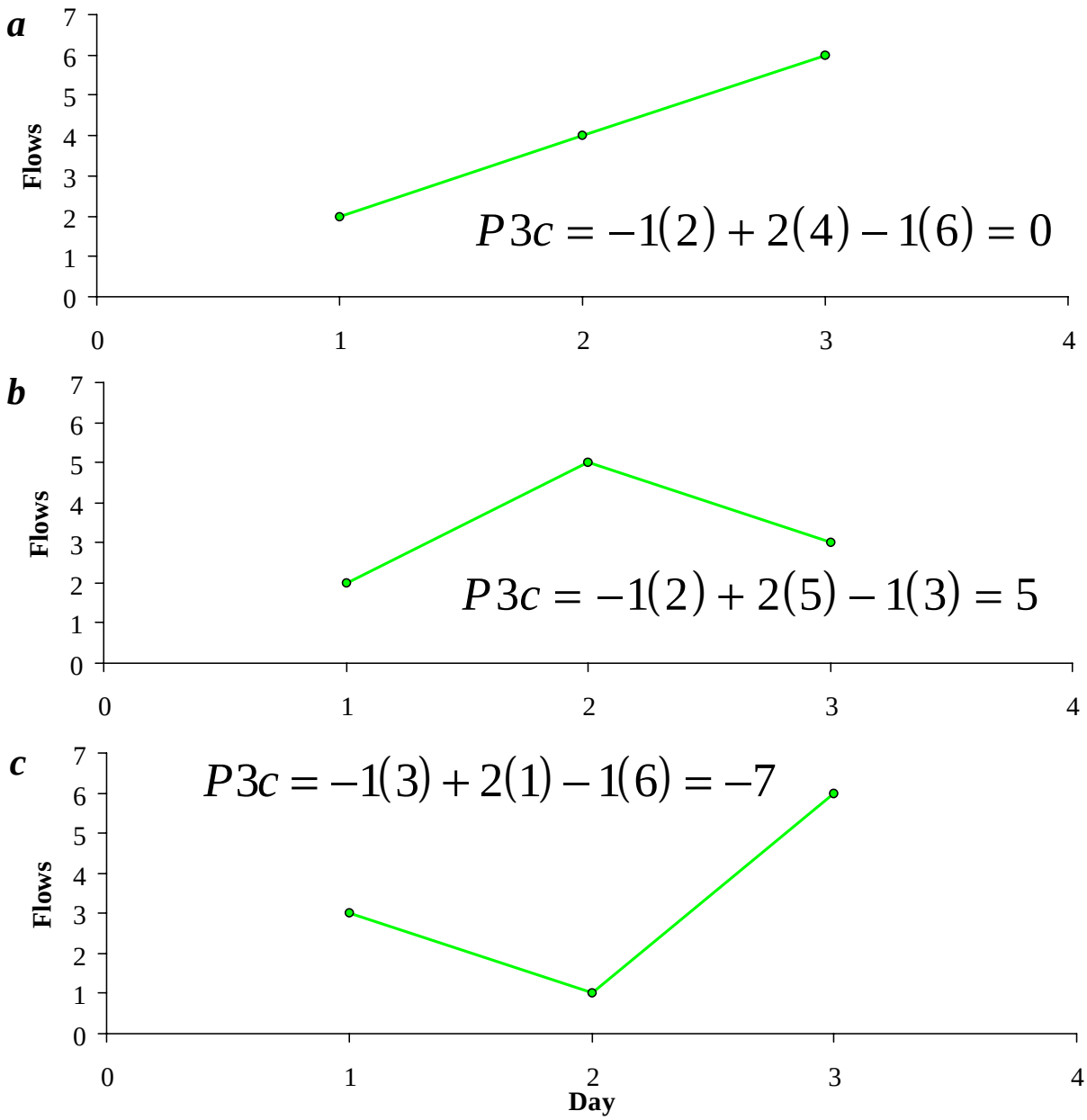


Figure 3: Time series of (***a***) daily flow, (***b***) *P5c* and (***c***) *P5* at LGR in 1994.

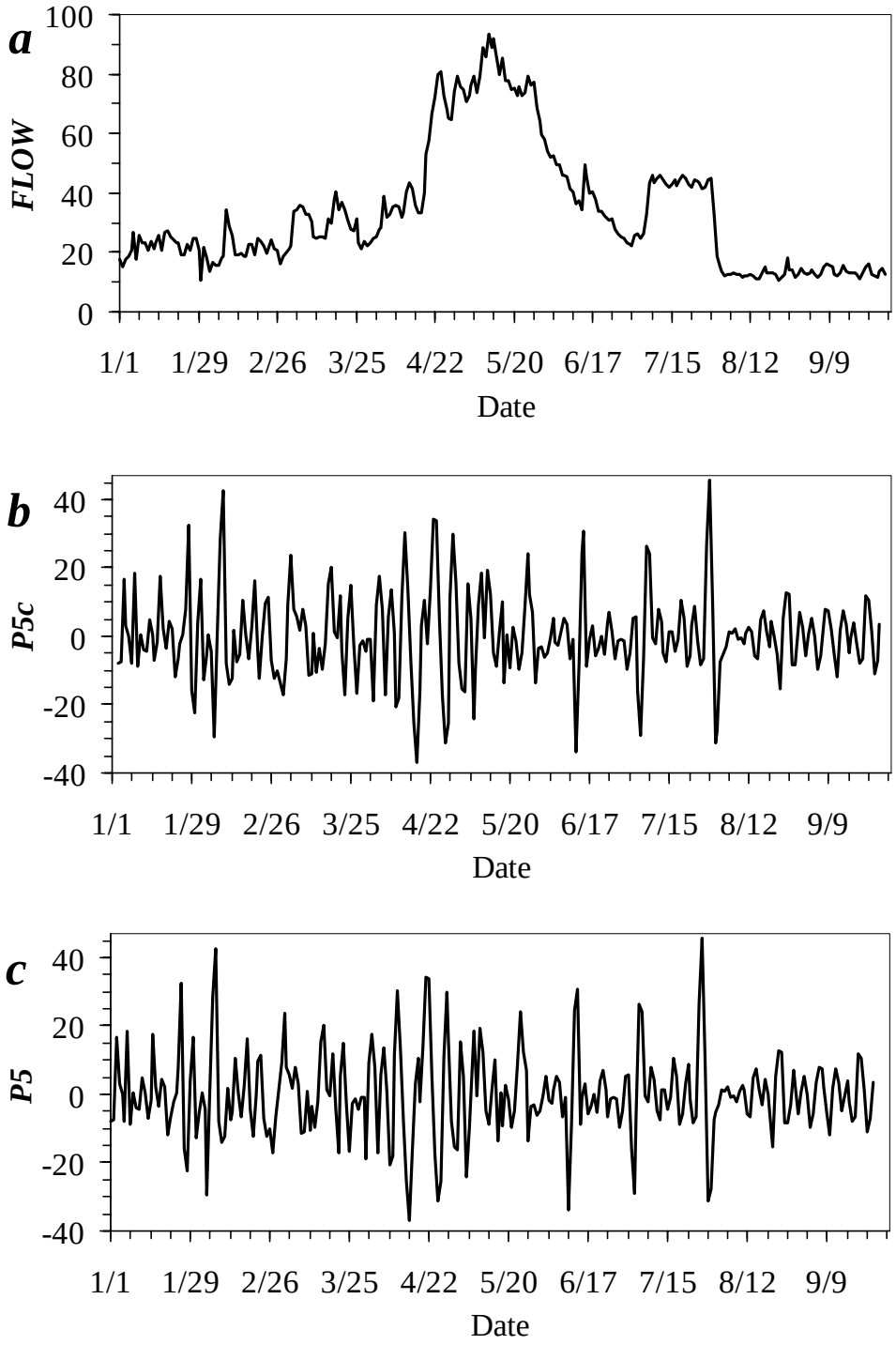
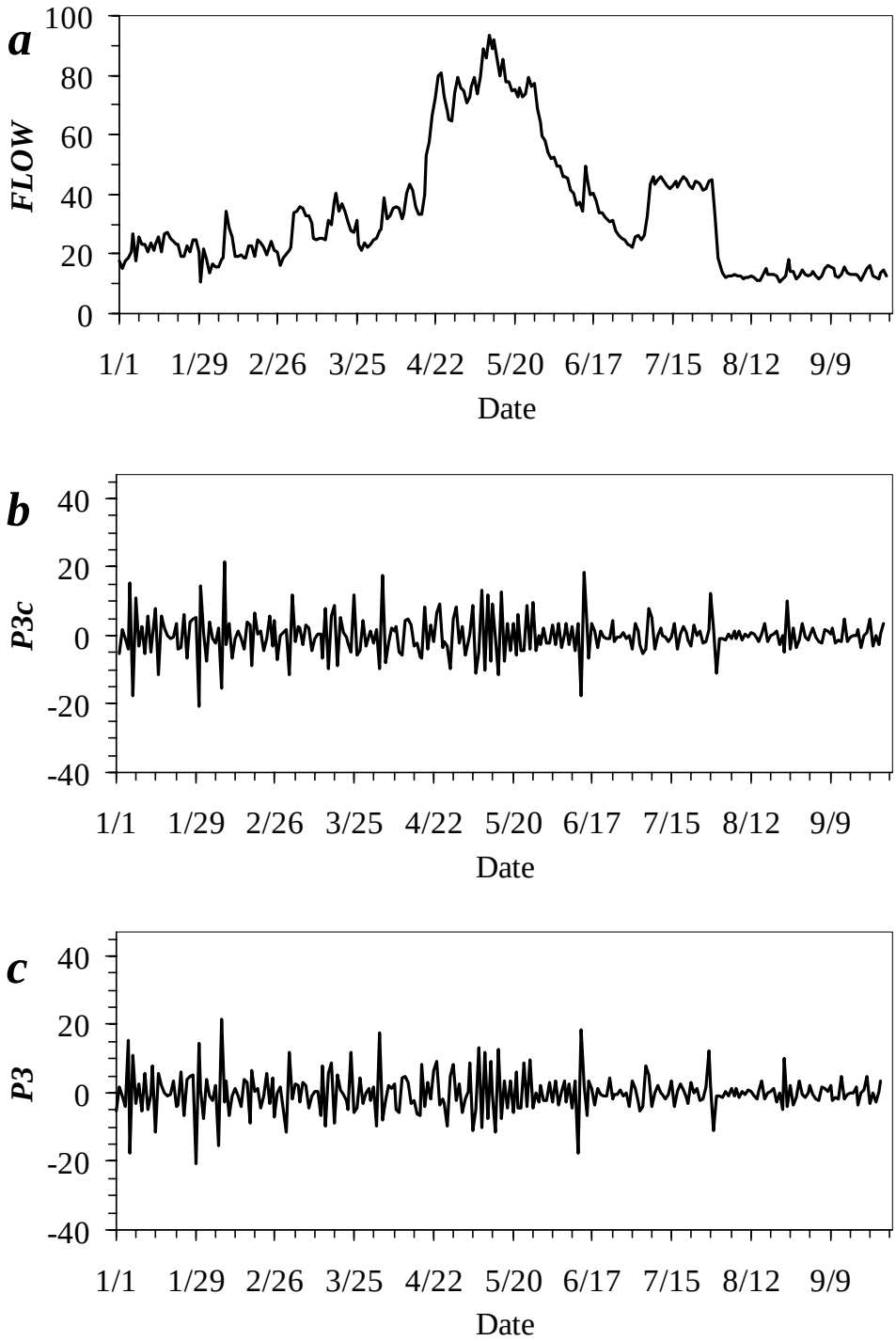


Figure 4: Time series of (***a***) daily flow , (***b***) *P3c* and (***c***) *P3* at LGR in 1994.



between flow and days after release, while the slope is a measure of the average flow change per day. The values of both slope and intercept will vary with the number of days considered in the regression (i.e., $k + 1$ days). Figure 5 illustrates this last feature, while Figure 6 compares the LGR flow time series to those for the slopes and intercepts estimated over three-day periods.

The slopes (α_1) and intercepts (α_o) for three different periods of $k + 1$ days were calculated and used as predictors. The periods were of 3, 6 and $\bar{TT}_j$ days ($\bar{TT}_j$ is the average travel time for fish group j). The corresponding linear coefficients were accordingly termed α_{13}, α_{o3}, α_{16}, α_{o6}, and α_{1TT}, α_{oTT}, respectively.

2.3.7 Polynomial coefficients

The previous procedure of describing the trends of flow change on release day by regression lines can further improved by using polynomial curve fitting. As before, let's take a sequence of flows F_j, where $j = 0, 1, 2, ..., k$ days after release, and $j = 0$ corresponding to a fish group release date. Then the sequence of flows over a period of $k + 1$ days can be represented by: $\hat{F}_i = \beta_o + \beta_1 j_i + \beta_2 j_i^2 + \beta_3 j_i^3 + \ldots + \beta_k j_i^k$, for $i = 1, 2, 3,..., k + 1$. The number of β coefficients and their estimated values vary with the length of the sequence k+1. We chose to fix this length in six days, because both the average and median travel times for all the marked fish used in the analysis were slightly over 5 days.

Finally, we also tried two predictors that were not flow related.

2.3.8 Average fish lengths (*L*)

All marked fish were measured at the time of their release, and they were rarely measured again at the downstream detection sites. In order to incorporate the relative fish size in our analysis, the initial lengths were averaged by fish group (*L*). It was expected that the harmonic mean speed (*HS*) would be larger with larger *L*'s. It was clear from the beginning that *L* was not

Figure 5: Linear regressions of flow versus days-after-release for nine fish released on May 12, 1994 at LGR. The regression lines were calculated for periods of 3 and 6 days from time of release.

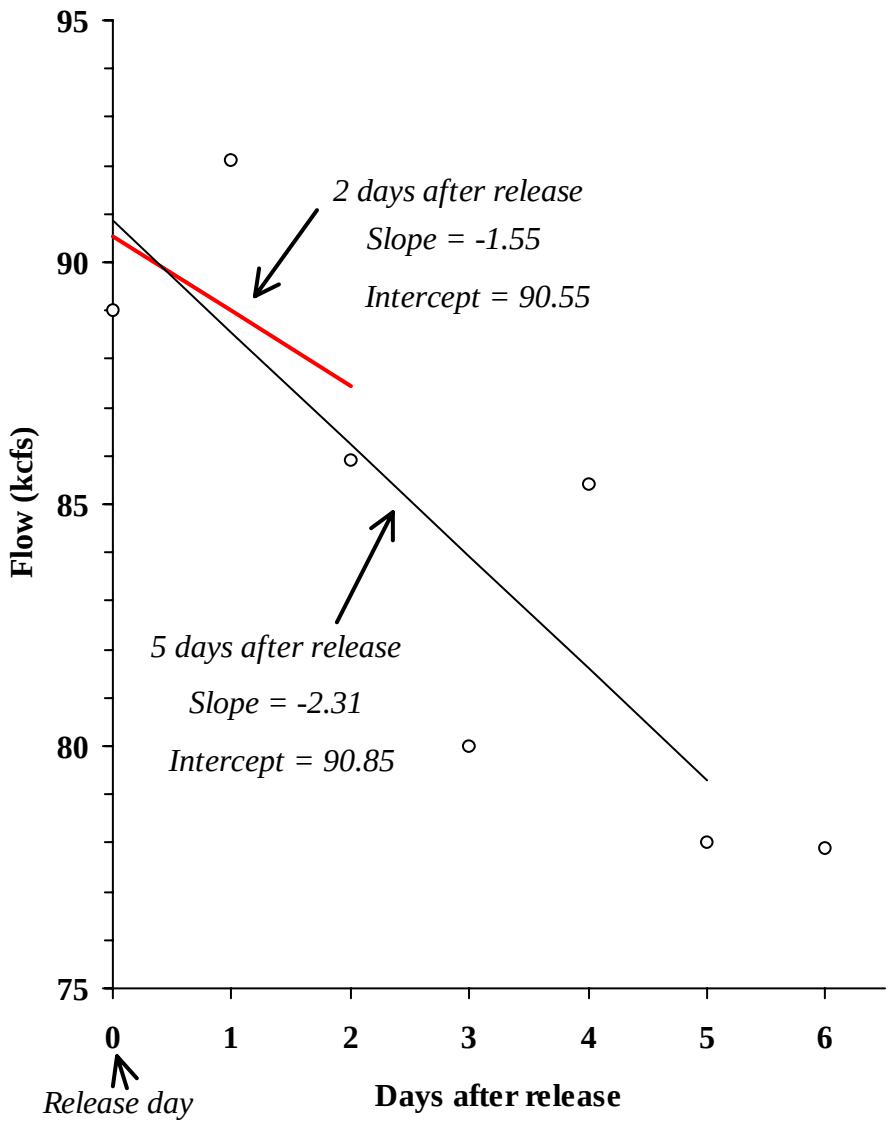
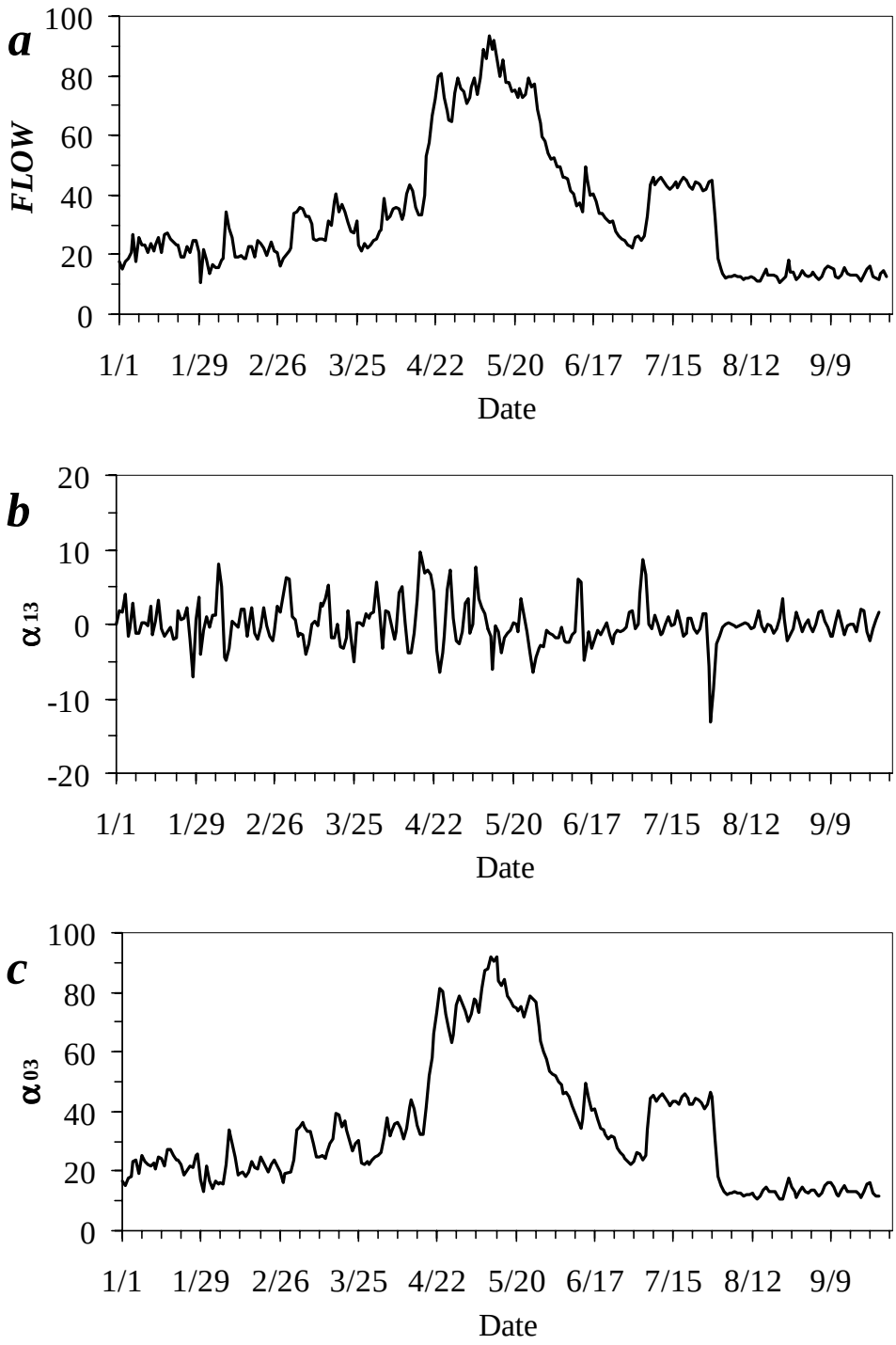


Figure 6: Time series of daily flow at LGR in 1994 and their corresponding slopes (α_{13}) and intercepts (α_{03}) for 3-day periods.



the best predictor to account for fish size effects because, among other reasons, *L* did not provide sufficient information on fish individual growth.

2.3.9 Group release date (*D*)

The date at which the fish group was last detected at LGR, LGS, or LMN, expressed in Julian days, was also incorporated as possible predictor. Although time is somewhat represented in other predictors (e.g., linear regression and polynomial coefficients), the release date was introduced in an attempt to capture the effects of other time related variables, such as water temperature, that may affect travel time.

2.4 Regression Models

Least squares regression analysis was used to find possible relationships between the harmonic mean speed of the fish groups (*HS*) and the above mentioned predictors. Given that the fish groups differed considerably in sample sizes (Table 1), thus affecting the values of *HS*, we used the sample size of the fish groups as weights in the least square minimization procedures.

The first step in the analysis was to test each predictor separately in a simple linear model $HS = b_o + b_1 X$, where *X* is any of the twenty predictors. Multiple regression analyses were performed next. Given that some predictors were highly correlated and carried redundant information, not all predictors were combined in multiple regression models. The following models were fitted:

$$HS = b_o + b_1 F + b_2 MF + b_3 FVAR + b_4 L + b_5 D \qquad \textbf{(M1)}$$

$$HS = b_o + b_1 Fch + b_2 F + b_3 L + b_4 D \qquad \textbf{(M2)}$$

$$HS = b_o + b_1 P3c + b_2 L + b_3 D \qquad \textbf{(M3)}$$

$$HS = b_o + b_1 P5c + b_2 L + b_3 D \qquad \textbf{(M3')}$$

$$HS = b_o + b_1 P3 + b_2 L + b_3 D \qquad \textbf{(M4)}$$

$$HS = b_o + b_1 P5 + b_2 L + b_3 D \qquad \textbf{(M4')}$$

$$HS = b_o + b_1 \alpha_{o3} + b_2 \alpha_{13} + b_3 L + b_4 D \qquad \textbf{(M5)}$$

$$HS = b_o + b_1 \alpha_{o6} + b_2 \alpha_{16} + b_3 L + b_4 D \qquad \textbf{(M6)}$$

$$HS = b_o + b_1 \alpha_{oTT} + b_2 \alpha_{1TT} + b_3 L + b_4 D \qquad \textbf{(M7)}$$

$$HS = b_o + b_1 \beta_o + b_2 \beta_1 + b_3 \beta_2 + b_4 \beta_3 + b_5 \beta_4 + b_6 \beta_5 + b_7 L + b_8 D \qquad \textbf{(M8)}$$

Finally, a forward stepwise selection of the variables included in the previous eight models was performed to obtain the "best" models. In this procedure, the most significant (α = 0.05) predictor is entered in the model first, and the remaining predictors are added to and deleted from the model until no additional variable can significantly improve the fit.

3. RESULTS

3.1 Distributions of Average Speed and Flow

Figures 7-9 illustrate the main temporal trends of flow and the response variable *HS* for each data subset. During the studied period (April 15 - July 20, 1994), the flow at LGR, LGS, and LMN dams (solid line in Figs. 7, 8 and 9) increased until May 1; it decreased from June 1 to July 1; and it increased again during the first days of July. Superimposed on this main trend, flow displayed smaller oscillations, probably accounted for by cyclic components at different frequencies. These smaller oscillations were more evident from May 1 to June 1. The response variable *HS* followed loosely the temporal trend of flow. For example, in the subsets LGR-LGS

Figure 7: Relationships between harmonic mean speed (*HS*, solid circles) and flow volume (line) for (***a***) hatchery and (***b***) wild fish in the LGR-LGS reach.

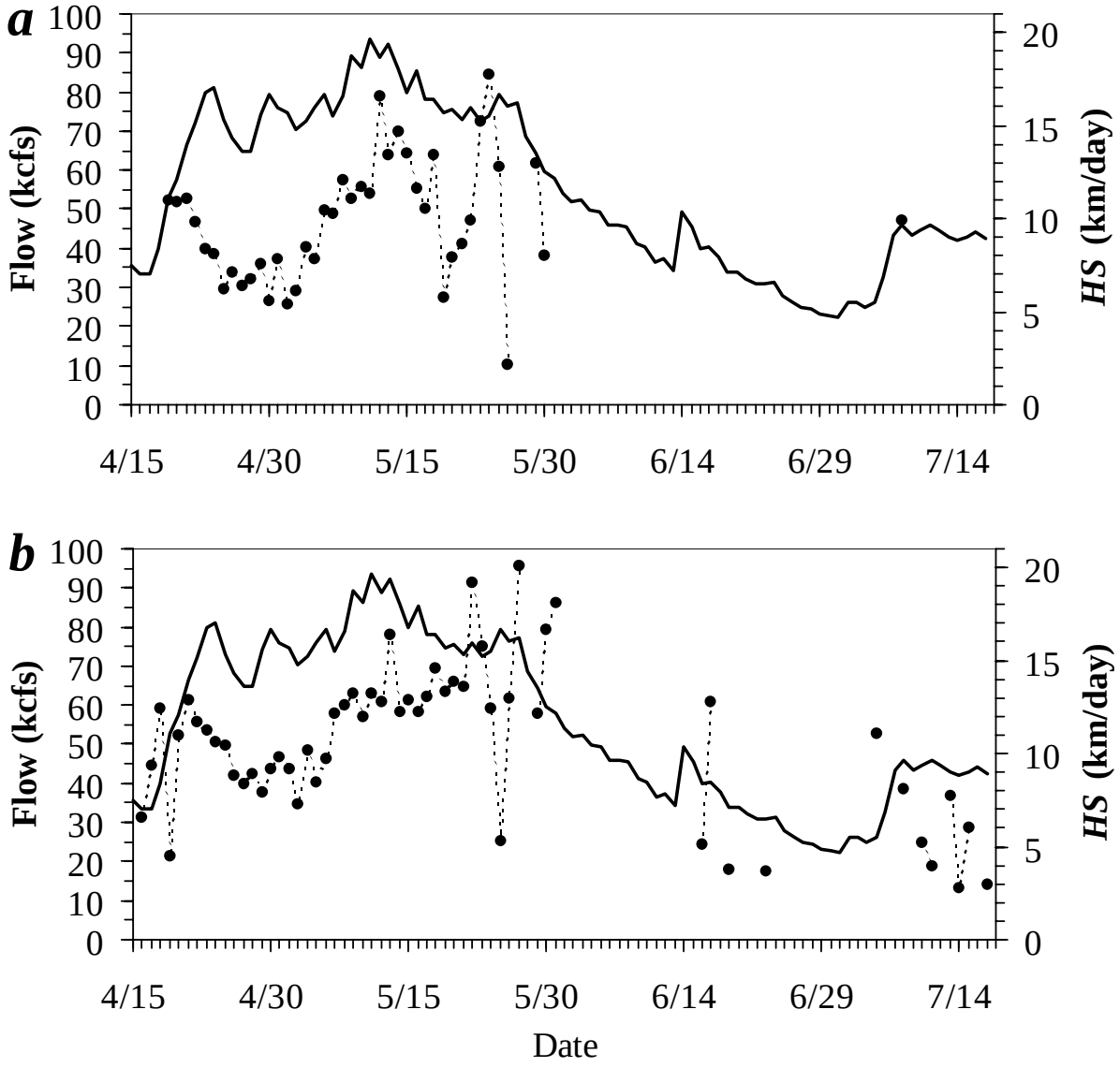


Figure 8: Relationships between harmonic mean speed (*HS*, solid circles) and flow volume (line) for (***a***) hatchery and (***b***) wild fish in the LGS-LMN reach.

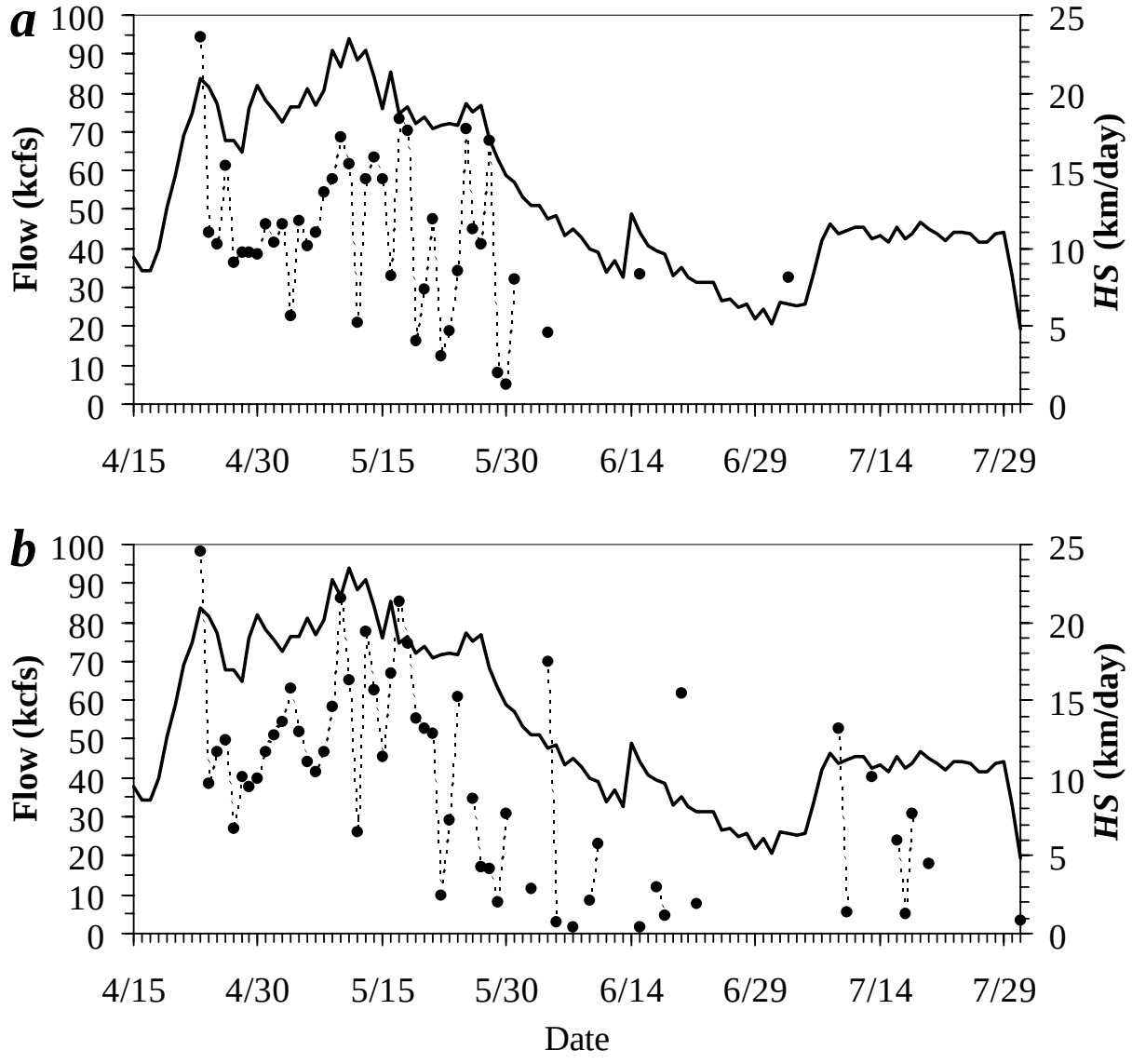
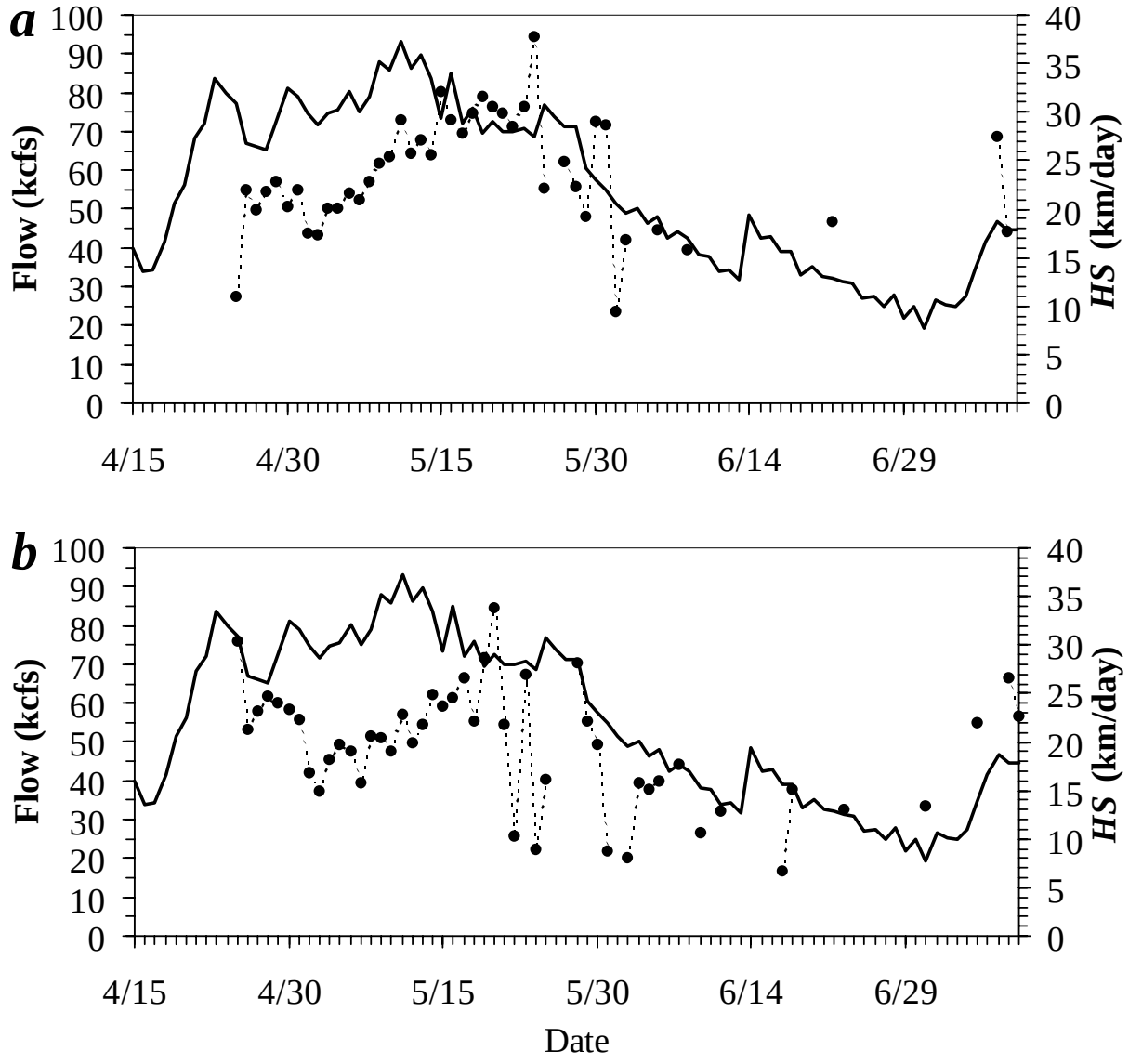


Figure 9: Relationships between harmonic mean speed (*HS*, solid circles) and flow volume (line) for (***a***) hatchery and (***b***) wild fish in the LMN-MCN reach.



H and LGR-LGS W (Figs. 7*a* and *b*, respectively), *HS* appeared to oscillate around some average value from April 20 to June 1, reflecting vaguely either the major trend or minor oscillations of flow during that period. In contrast, the LGS-LMN subsets (Fig. 8) seemed to reflect better the minor flow oscillations occurring from May 1 to June 1. Finally, for the LMN-MCN subsets, *HS* seemed to follow quite well the major trend of increasing flows perceived in May and more loosely, the decreasing trend of June. This pattern is especially noticeable with hatchery fish (Fig. 9*a*).

The number of fish per release date was very different among reaches. While the period June 1 - July 20 was rarely sampled in all reaches, large sample sizes occurred during the last week of April and by mid-May in the LGR-LGS reach (10 to 70 PIT-tagged fish), around May 1 in the LGS-LMN reach (15 to 50 fish), and during most of May in the LMN-MCN reach (15 to 90 tagged fish). Given the large dispersion of individual fish speeds (Fig. 1), *HS*, as any other measure of central tendency for fish speeds, may have been imprecisely estimated by small sample sizes.

3.2 Regression Analyses

Tables 2-7 display the estimates of intercept $(\hat{b}_o)$ and slope $(\hat{b}_1)$ for the simple linear models $HS = b_o + b_1 X$, where *X* being any of the twenty different predictors described in previous section. Albeit inconsistently across subsets, *HS* showed significant ($\alpha < 0.05$) linear relationships with some of the flow-related predictors. Flow on release day, *F*, was significant for three data subsets, LGR-LGS H, LGR-LGS W, and LGS-LMN W. The intercepts of the regressions between flow and time (α_{o3}, α_{o6}, and α_{oTT}) and that of the polynomial regression (β_o), that could be interpreted as proxy for flow on release day, were significant for the same three data subsets for which *F* was. Averaged mean daily flow, *MF*, was also significant for the same three subsets, and nearly so in another (LGS-LMN H, Prob. = 0.052). Measures of the linear trend of

Table 2: Intercept $(\hat{b}_o)$ and slope $(\hat{b}_1)$ estimates for the 22 simple regressions between *HS* and predictor variables *X* for hatchery smolt chinook in the LGR-LGS reach. See text for definitions of predictor variables *X*.

X	$\hat{b}_o$	SE $(\hat{b}_o)$	P-Value	$\hat{b}_1$	SE $(\hat{b}_1)$	P-Value	r^2
F	-2.547	3.421	0.461	0.153	0.044	0.001	0.241
MF	-7.776	4.019	0.060	0.220	0.052	0.000	0.323
FVAR	10.083	0.961	0.000	-0.030	0.032	0.354	0.023
Fch	9.296	0.417	0.000	-0.026	0.038	0.502	0.012
P3c	9.263	0.420	0.000	0.008	0.058	0.897	0.000
P3	9.244	0.416	0.000	0.046	0.060	0.451	0.015
P5c	9.276	0.437	0.000	-0.001	0.023	0.957	0.000
P5	9.205	0.381	0.000	0.052	0.019	0.008	0.171
α_{o3}	-3.022	3.390	0.378	0.159	0.044	0.001	0.259
α_{13}	9.276	0.406	0.000	0.147	0.098	0.144	0.055
α_{o6}	-6.479	2.806	0.026	0.204	0.036	0.000	0.456
α_{16}	9.173	0.397	0.000	-0.426	0.200	0.039	0.107
α_{oTT}	-7.165	2.821	0.015	0.214	0.037	0.000	0.475
α_{1TT}	9.320	0.399	0.000	-0.418	0.213	0.057	0.092
β_o	-2.547	3.421	0.461	0.153	0.044	0.001	0.241
β_1	9.269	0.416	0.000	0.009	0.018	0.622	0.006
β_2	9.269	0.418	0.000	-0.001	0.012	0.915	0.000
β_3	9.270	0.418	0.000	0.002	0.021	0.937	0.000
β_4	9.271	0.418	0.000	-0.014	0.095	0.883	0.001
β_5	9.272	0.418	0.000	0.255	1.196	0.832	0.001
L	26.801	6.739	0.000	-0.139	0.054	0.013	0.152
D	-233422.819	67603.716	0.001	0.133	0.039	0.001	0.239

Table 3: Intercept $(\hat{b}_o)$ and slope estimates $(\hat{b}_1)$ for the 22 simple regressions between *HS* and predictor variables *X* for wild smolt chinook in the LGR-LGS reach. See text for definitions of predictor variables *X*.

X	$\hat{b}_o$	SE $(\hat{b}_o)$	P-Value	$\hat{b}_1$	SE $(\hat{b}_1)$	P-Value	r^2
F	3.779	1.933	0.056	0.096	0.026	0.000	0.200
MF	2.678	2.210	0.231	0.110	0.029	0.000	0.203
FVAR	11.127	0.441	0.000	-0.008	0.011	0.477	0.009
Fch	10.893	0.295	0.000	0.001	0.019	0.943	0.000
P3c	10.878	0.291	0.000	0.017	0.043	0.701	0.003
P3	10.853	0.293	0.000	0.031	0.044	0.495	0.009
P5c	10.802	0.302	0.000	0.014	0.015	0.352	0.016
P5	10.830	0.288	0.000	0.020	0.015	0.179	0.033
α_{o3}	3.778	1.910	0.053	0.096	0.025	0.000	0.204
α_{13}	10.888	0.290	0.000	0.001	0.068	0.988	0.000
α_{o6}	2.419	1.875	0.202	0.113	0.025	0.000	0.274
α_{16}	10.810	0.280	0.000	-0.284	0.126	0.028	0.085
α_{oTT}	2.747	1.923	0.159	0.109	0.026	0.000	0.249
α_{1TT}	10.879	0.284	0.000	-0.178	0.114	0.125	0.042
β_o	3.779	1.933	0.056	0.096	0.026	0.000	0.200
β_1	10.884	0.290	0.000	0.004	0.015	0.787	0.001
β_2	10.889	0.290	0.000	-0.001	0.010	0.909	0.000
β_3	10.889	0.290	0.000	0.001	0.017	0.962	0.000
β_4	10.889	0.290	0.000	-0.004	0.076	0.954	0.000
β_5	10.890	0.290	0.000	0.076	0.952	0.937	0.000
L	7.095	2.268	0.003	0.046	0.027	0.098	0.049
D	14572.504	35867.156	0.686	-0.008	0.020	0.686	0.003

Table 4: Intercept $(\hat{b}_o)$ and slope estimates $(\hat{b}_1)$ for the 22 simple regressions between *HS* and predictor variables *X* for hatchery smolt chinook in the LGS-LMN reach. See text for definitions of predictor variables *X*.

X	$\hat{b}_o$	SE $(\hat{b}_o)$	P-Value	$\hat{b}_1$	SE $(\hat{b}_1)$	P-Value	r^2
F	5.281	5.318	0.327	0.076	0.069	0.280	0.029
MF	-0.342	5.722	0.953	0.150	0.075	0.052	0.091
FVAR	11.425	0.840	0.000	-0.018	0.034	0.599	0.007
Fch	11.244	0.516	0.000	-0.037	0.019	0.059	0.086
P3c	11.105	0.524	0.000	-0.070	0.059	0.240	0.034
P3	11.110	0.533	0.000	0.036	0.058	0.536	0.010
P5c	11.085	0.533	0.000	0.007	0.026	0.796	0.002
P5	11.089	0.537	0.000	0.005	0.031	0.876	0.001
α_{o3}	11.089	0.537	0.000	0.005	0.031	0.876	0.001
α_{13}	11.059	0.529	0.000	-0.114	0.145	0.437	0.015
α_{o6}	4.402	5.505	0.429	0.088	0.072	0.230	0.036
α_{16}	11.127	0.530	0.000	-0.243	0.272	0.378	0.020
α_{oTT}	4.287	5.286	0.422	0.089	0.069	0.204	0.040
α_{1TT}	11.077	0.530	0.000	-0.107	0.165	0.519	0.010
β_o	5.281	5.318	0.327	0.076	0.069	0.280	0.029
β_1	11.110	0.525	0.000	0.020	0.018	0.269	0.030
β_2	11.099	0.522	0.000	-0.015	0.011	0.194	0.042
β_3	11.091	0.521	0.000	0.029	0.021	0.176	0.045
β_4	11.088	0.520	0.000	-0.128	0.091	0.170	0.047
β_5	11.086	0.520	0.000	1.601	1.141	0.168	0.047
L	8.741	10.170	0.395	0.018	0.080	0.819	0.001
D	-48522.145	100188.584	0.631	0.028	0.057	0.631	0.006

Table 5: Intercept $(\hat{b}_o)$ and slope estimates $(\hat{b}_1)$ for the 22 simple regressions between *HS* and predictor variables *X* for wild smolt chinook in the LGS-LMN reach. See text for definitions of predictor variables *X*.

X	$\hat{b}_o$	SE $(\hat{b}_o)$	P-Value	$\hat{b}_1$	SE $(\hat{b}_1)$	P-Value	r^2
F	-5.292	3.313	0.116	0.223	0.045	0.000	0.317
MF	-4.710	2.626	0.078	0.219	0.036	0.000	0.409
FVAR	12.517	0.711	0.000	-0.073	0.023	0.002	0.158
Fch	11.230	0.616	0.000	0.040	0.043	0.365	0.015
P3c	11.100	0.603	0.000	-0.017	0.076	0.825	0.001
P3	11.135	0.604	0.000	0.047	0.075	0.531	0.007
P5c	11.120	0.599	0.000	0.029	0.030	0.350	0.016
P5	11.045	0.613	0.000	-0.015	0.033	0.655	0.004
α_{o3}	11.045	0.613	0.000	-0.015	0.033	0.655	0.004
α_{13}	11.076	0.606	0.000	-0.056	0.166	0.737	0.002
α_{o6}	-4.973	3.314	0.139	0.221	0.045	0.000	0.308
α_{16}	11.085	0.609	0.000	0.042	0.322	0.897	0.000
α_{oTT}	-4.337	3.125	0.171	0.210	0.042	0.000	0.317
α_{1TT}	11.057	0.615	0.000	-0.060	0.184	0.746	0.002
β_o	-5.292	3.313	0.116	0.223	0.045	0.000	0.317
β_1	11.105	0.603	0.000	0.008	0.023	0.739	0.002
β_2	11.098	0.603	0.000	-0.004	0.015	0.790	0.001
β_3	11.096	0.603	0.000	0.005	0.027	0.867	0.001
β_4	11.096	0.603	0.000	-0.010	0.118	0.931	0.000
β_5	11.096	0.603	0.000	0.039	1.481	0.979	0.000
L	14.406	4.853	0.004	-0.040	0.058	0.495	0.009
D	143117.139	60307.269	0.021	-0.082	0.034	0.021	0.094

Table 6: Intercept $(\hat{b}_o)$ and slope estimates $(\hat{b}_1)$ for the 22 simple regressions between *HS* and predictor variables *X* for hatchery smolt chinook in the LMN-MCN reach. See text for definitions of predictor variables *X*.

X	$\hat{b}_o$	SE $(\hat{b}_o)$	P-Value	$\hat{b}_1$	SE $(\hat{b}_1)$	P-Value	r^2
F	18.505	6.574	0.007	0.081	0.084	0.345	0.022
MF	28.218	7.099	0.000	-0.044	0.091	0.626	0.006
FVAR	25.430	1.301	0.000	-0.030	0.048	0.542	0.009
Fch	24.797	0.701	0.000	0.001	0.003	0.627	0.006
P3c	24.726	0.694	0.000	-0.045	0.066	0.504	0.011
P3	24.686	0.694	0.000	0.058	0.065	0.372	0.020
P5c	24.779	0.699	0.000	-0.017	0.044	0.694	0.004
P5	24.718	0.689	0.000	0.048	0.046	0.305	0.026
α_{o3}	24.718	0.689	0.000	0.048	0.046	0.305	0.026
α_{13}	24.756	0.672	0.000	-0.362	0.207	0.088	0.070
α_{o6}	16.913	6.641	0.015	0.101	0.085	0.242	0.033
α_{16}	24.558	0.610	0.000	-1.159	0.322	0.001	0.241
α_{oTT}	15.773	6.811	0.026	0.116	0.087	0.192	0.041
α_{1TT}	24.743	0.599	0.000	-1.198	0.314	0.000	0.262
β_o	18.505	6.574	0.007	0.081	0.084	0.345	0.022
β_1	24.721	0.693	0.000	0.014	0.018	0.452	0.014
β_2	24.727	0.691	0.000	-0.010	0.012	0.392	0.018
β_3	24.735	0.691	0.000	0.018	0.021	0.401	0.017
β_4	24.740	0.691	0.000	-0.080	0.094	0.397	0.018
β_5	24.744	0.691	0.000	1.029	1.181	0.389	0.018
L	48.726	12.253	0.000	-0.187	0.095	0.057	0.086
D	-529430.116	120832.231	0.000	0.302	0.069	0.000	0.319

Table 7: Intercept $(\hat{b}_o)$ and slope estimates $(\hat{b}_1)$ for the 22 simple regressions between *HS* and predictor variables *X* for wild smolt chinook in the LMN-MCN reach. See text for definitions of predictor variables *X*.

X	$\hat{b}_o$	SE $(\hat{b}_o)$	P-Value	$\hat{b}_1$	SE $(\hat{b}_1)$	P-Value	r^2
F	16.471	4.345	0.000	0.063	0.057	0.270	0.027
MF	18.471	4.630	0.000	0.037	0.060	0.545	0.008
FVAR	22.846	1.094	0.000	-0.061	0.035	0.092	0.062
Fch	21.573	0.603	0.000	0.002	0.001	0.033	0.097
P3c	21.169	0.615	0.000	0.077	0.066	0.248	0.029
P3	21.209	0.632	0.000	-0.034	0.074	0.654	0.005
P5c	21.287	0.619	0.000	0.012	0.036	0.745	0.002
P5	21.238	0.620	0.000	0.020	0.038	0.610	0.006
α_{o3}	21.238	0.620	0.000	0.020	0.038	0.610	0.006
α_{13}	21.329	0.620	0.000	-0.116	0.163	0.478	0.011
α_{o6}	16.857	4.465	0.000	0.058	0.058	0.324	0.022
α_{16}	21.324	0.607	0.000	-0.440	0.323	0.179	0.040
α_{oTT}	17.228	4.340	0.000	0.053	0.056	0.352	0.019
α_{1TT}	21.245	0.609	0.000	-0.315	0.270	0.250	0.029
β_o	16.471	4.345	0.000	0.063	0.057	0.270	0.027
β_1	21.230	0.627	0.000	-0.008	0.020	0.709	0.003
β_2	21.251	0.627	0.000	0.002	0.012	0.842	0.001
β_3	21.261	0.625	0.000	-0.003	0.022	0.903	0.000
β_4	21.268	0.623	0.000	0.004	0.096	0.966	0.000
β_5	21.274	0.622	0.000	0.041	1.188	0.972	0.000
L	15.423	4.394	0.001	0.068	0.051	0.186	0.039
D	80552.967	96711.837	0.409	-0.046	0.055	0.409	0.015

flow with time, such as α_{16} and α_{1TT}, proved significant for LGR-LGS, both H and W, and LMN-MCN H. Finally, *HS* showed a significant ($\alpha < 0.05$) linear relationship with a measure of flow dispersion, *FVAR*, in one occasion, LGS-LMN W. The average flow change, *Fch*, proved to be significant also in only one occasion, LMN-MCN W. The variables *P3c*, *P5c*, *P3* and *P5*, especially designed to measure relative changes of flow level on release day relative to short periods of 3 and 5 days did not prove to be significantly correlated with *HS* in most reaches. Only for the hatchery chinook in the LGR-LGS reach was *P5* significantly correlated with *HS* (Prob. = 0.008). The two predictors not related to flow, *L* and *D*, did show significant linear relationships with data subsets: LGR-LGS H for *L*, and LGR-LGS H, LGS-LMN W, and LMN-MCN H for *D*.

Tables 8-10 display the results of fitting the ten multiple regression models chosen for the present study. Tables 11-13 present the equations for the models selected by the forward stepwise procedure. In some cases,none of the predictor variables combined in the ten multiple regression models significantly improved the fit to the data. In those cases, the stepwise procedure selected the weighted average of *HS* as “best” model. The weighted average of *HS* was equal to 9.268 and 10.889 km/day for the LGR-LGS H and LGR-LGS W data, respectively. The weighted average for HS was 11.079 km/day for LGS-LMN H and 11.096 km/day for LGS-LMN W. For LMN-MCN, it took the values of 24.754 and 21.272 km/day for hatchery and wild fish, respectively. One noticeable example of failing to significantly improve the fit to the data is given by the variables *P3c*, *P5c*, *P3* and *P5* that were combined with *L* and *D* in models M3, M3’, M4 and M4’ (Tables 11, 12, and 13). These flow-related variables were not selected by the stepwise regression procedure for any but one case (model M4’ for LGR-LGS H data). The stepwise procedure had more difficulty in finding adequate combinations of predictor variables for the LMN-MCN W data (Table 13). For the remaining data, the stepwise regression procedure selected variable subsets containing at least one flow related.

Table 8: Multiple regression fits for (***a***) hatchery and (***b***) wild smolt chinook in the LGR-LGS reach. See text for definitions of predictor variables.

a

Model	Fit	r^2
M1	$HS = -252831.523 + 0.053F + 0.134MF + 0.035FVAR + 0.064L + 0.144D$	0.441
M2	$HS = -281757.283 + 0.144F - 0.049Fch + 0.121L + 0.160D$	0.405
M3	$HS = -383615.668 + 0.026P3c + 0.123L + 0.219D$	0.261
M3’	$HS = -412309.025 + 0.020P5c + 0.136L + 0.235D$	0.273
M4	$HS = -361767.850 + 0.052P3 + 0.103L + 0.206D$	0.275
M4’	$HS = -320763.201 + 0.050P5 + 0.075L + 0.183D$	0.410
M5	$HS = -217528.810 + 0.183\alpha_{o3} + 0.269\alpha_{13} + 0.082L + 0.124D$	0.532
M6	$HS = -295003.154 + 0.172\alpha_{o6} - 0.031\alpha_{16} + 0.148L + 0.168D$	0.533
M7	$HS = -262715.441 + 0.190\alpha_{oTT} + 0.027\alpha_{1TT} + 0.133L + 0.150D$	0.538
M8	$HS = -226485.818 + 0.142\beta_o - 0.168\beta_1 - 1.907\beta_2 - 12.138\beta_3 - 67.833\beta_4 - 360.398\beta_5 + 0.091L + 0.129D$	0.595

b

Model	Fit	r^2
M1	$HS = -66604.115 + 0.065F + 0.074MF + 0.008FVAR + 0.056L + 0.038D$	0.310
M2	$HS = -45204.309 - 0.012Fch + 0.109F + 0.057L + 0.026D$	0.279
M3	$HS = -7246.681 + 0.013P3c + 0.047L + 0.004D$	0.051
M3’	$HS = -10215.810 + 0.011P5c + 0.045L + 0.006D$	0.058
M4	$HS = -5475.212 + 0.020P3 + 0.045L + 0.003D$	0.053
M4’	$HS = -3966.209 + 0.012P5 + 0.038L + 0.002D$	0.061
M5	$HS = -49197.088 + 0.126\alpha_{o3} + 0.114\alpha_{13} + 0.047L + 0.028D$	0.310
M6	$HS = -45175.598 + 0.122\alpha_{o6} + 0.044\alpha_{16} + 0.044L + 0.026D$	0.320
M7	$HS = -44436.140 + 0.123\alpha_{oTT} + 0.080\alpha_{1TT} + 0.048L + 0.025D$	0.304
M8	$HS = -37467.380 + 0.118\beta_o - 0.071\beta_1 - 0.873\beta_2 - 5.942\beta_3 - 34.517\beta_4 - 187.640\beta_5 + 0.039L + 0.021D$	0.337

Table 9: Multiple regression fits for (***a***) hatchery and (***b***) wild smolt chinook in the LGS-LMN reach. See text for definitions of predictor variables.

a

Model	Fit	r^2
M1	$HS = -168069.282 - 0.103F + 0.239MF - 0.008FVAR + 0.056L + 0.096D$	0.133
M2	$HS = -144874.049 + 0.119F - 0.053Fch + 0.070L + 0.083D$	0.190
M3	$HS = -146266.954 - 0.071P3c + 0.109L + 0.083D$	0.060
M3'	$HS = -144095.035 - 0.0003P5c + 0.103L + 0.082D$	0.025
M4	$HS = -14343.828 + 0.083P3 + 0.109L + 0.082D$	0.035
M4'	$HS = -146728.515 + 0.008P5 + 0.108L + 0.084D$	0.026
M5	$HS = -94776.995 + 0.064\alpha_{o3} - 0.020\alpha_{13} + 0.062L + 0.054D$	0.046
M6	$HS = -92591.114 + 0.065\alpha_{o6} - 0.053\alpha_{16} + 0.069L + 0.053D$	0.047
M7	$HS = -99083.201 + 0.073\alpha_{oTT} - 0.010\alpha_{1TT} + 0.064L + 0.056D$	0.050
M8	$HS = -19778.759 + 0.084\beta_o - 0.281\beta_1 - 1.922\beta_2 - 11.61\beta_3 - 65.193\beta_4 - 349.227\beta_5 + 0.029L + 0.011D$	0.127

b

Model	Fit	r^2
M1	$HS = -9376654 - 0.016F + 0.262MF - 0.033FVAR - 0.046L + 0.053D$	0.487
M2	$HS = 71608.176 + 0.195F + 0.007Fch - 0.099L - 0.041D$	0.348
M3	$HS = 257721.415 - 0.028P3c - 0.182L - 0.147D$	0.211
M3'	$HS = 254834.144 + 0.023P5c - 0.173L - 0.145D$	0.219
M4	$HS = 255370.490 + 0.032P3 - 0.177L - 0.145D$	0.212
M4'	$HS = 261569.697 - 0.031P5 - 0.196L - 0.149D$	0.223
M5	$HS = 50758.417 + 0.210\alpha_{o3} + 0.048\alpha_{13} - 0.088L - 0.029D$	0.354
M6	$HS = -287.985 + 0.237\alpha_{o6} + 0.463\alpha_{16} - 0.077L + 0.0002D$	0.350
M7	$HS = 57345.123 + 0.197\alpha_{oTT} + 0.045\alpha_{1TT} - 0.101L - 0.033D$	0.355
M8	$HS = -16633.656 + 0.257\beta_o + 0.581\beta_1 + 2.945\beta_2 + 14.446\beta_3 + 69.395\beta_4 + 331.393\beta_5 - 0.102L + 0.009D$	0.393

Table 10: Multiple regression fits for (***a***) hatchery and (***b***) wild smolt chinook in the LMN-MCN reach. See text for definitions of predictor variables.

a

Model	Fit	r^2
M1	$HS = -922664.811 + 0.117F + 0.137MF - 0.063FVAR + 0.235L + 0.526D$	0.481
M2	$HS = -803359.345 + 0.187F - 0.002Fch + 0.172L + 0.458D$	0.448
M3	$HS = -646473.675 - 0.023P3c + 0.116L + 0.368D$	0.342
M3'	$HS = -660457.885 - 0.014P5c + 0.129L + 0.376D$	0.342
M4	$HS = -631831.637 - 0.043P3 + 0.101L + 0.360D$	0.349
M4'	$HS = -664496.925 + 0.062P5 + 0.114L + 0.379D$	0.381
M5	$HS = -867575.617 + 0.240\alpha_{o3} + 0.234\alpha_{13} + 0.180L + 0.494D$	0.474
M6	$HS = -758713.056 + 0.194\alpha_{o6} - 0.170\alpha_{16} + 0.162L + 0.432D$	0.482
M7	$HS = -735861.742 + 0.205\alpha_{oTT} - 0.195\alpha_{1TT} + 0.153L + 0.419D$	0.489
M8	$HS = -723798.750 + 0.196\beta_o - 0.035\beta_1 - 0.760\beta_2 - 2.052\beta_3 + 1.854\beta_4 + 64.220\beta_5 + 0.102L + 0.412D$	0.527

b

Model	Fit	r^2
M1	$HS = 31099.669 + 0.173F - 0.123MF - 0.060FVAR + 0.072L - 0.018D$	0.154
M2	$HS = -20992.811 + 0.071F + 0.002Fch + 0.074L - 0.012D$	0.161
M3	$HS = 35264.305 + 0.088P3c + 0.067L - 0.020D$	0.079
M3'	$HS = 30706.124 + 0.016P5c + 0.063L - 0.017D$	0.044
M4	$HS = 29163.366 - 0.033P3 + 0.061L - 0.017D$	0.045
M4'	$HS = 26146.349 + 0.014P5 + 0.060L - 0.015D$	0.043
M5	$HS = -8334.083 + 0.059\alpha_{o3} - 0.118\alpha_{13} + 0.083L + 0.005D$	0.080
M6	$HS = 84563.453 + 0.004\alpha_{o6} - 0.650\alpha_{16} + 0.074L - 0.048D$	0.117
M7	$HS = 80776.139 - 0.004\alpha_{oTT} - 0.511\alpha_{1TT} + 0.076L - 0.046D$	0.104
M8	$HS = 92774.431 - 0.005\beta_o - 0.612\beta_1 - 2.523\beta_2 - 9.114\beta_3 - 29.222\beta_4 - 77.000\beta_5 + 0.075L - 0.053D$	0.191

Table 11: Models selected by forward stepwise procedure for LGR-LGS data. Standard errors for regression coefficients are given in parentheses. See text for variables included in models M1 to M8.

For variables in model	Models selected LGR-LGS Hatchery *HS*	r^2	LGR-LGS Wild *HS*	r^2
M1	*-146317.307+0.171MF+0.083D*	0.401	*2.678+0.110MF*	0.203
	(66740.985) (0.054) (0.038)		*(2.210) (0.029)*	
M2	*-136180.099+0.141F-0.058 Fch+0.078D*	0.387	*-0.115+0.096F+0.047L*	0.251
	(70612.604) (0.049) (0.034) (0.040)		*(2.773)(0.025) (0.024)*	
M3	*-233422.819+0.133D*	0.239	*10.889*	
	(67603.716) (0.039)		*(0.287)*	
M3’	*-233422.819+0.133D*	0.239	*10.889*	
	(67603.716) (0.039)		*(0.287)*	
M4	*-233422.819+0.133D*	0.239	*10.889*	
	(67603.716) (0.039)		*(0.287)*	
M4’	*-229925.086+0.051P5+0.131D*	0.403	*10.889*	
	(60692.766) (0.016) (0.035)		*(0.287)*	
M5	$-119120.102+0.181\alpha_{o3}+0.285\ \alpha_{13}+0.068D$	0.524	$2.028+0.119\alpha_{o3}+0.125\alpha_{13}$	0.254
	(61508.480) (0.044) (0.079) (0.035)		*(2.081)(0.028) (0.066)*	
M6	$-116618.712+0.172\alpha_{o6}+0.066D$	0.505	$2.419+0.113\alpha_{o6}$	0.274
	(61149.680) (0.039) (0.039)		*(1.875)(0.025)*	
M7	$-7.165+0.214\alpha_{oTT}$	0.475	$2.747+0.109\alpha_{oTT}$	0.249
	(2.821) (0.037)		*(1.923)(0.026)*	
M8	$-163377.297+0.108\beta_o+0.093D$	0.337	$-0.115+0.096\beta_o+0.047L$	0.251
	(70598.248) (0.046) (0.040)		*(2.773)(0.025) (0.024)*	

Table 12: Models selected by forward stepwise procedure for LGS-LMN data. Standard errors for regression coefficients are given in parentheses. See text for variables included in models M1 to M8.

For variables in model	Models selected LGS-LMN Hatchery *HS*	r^2	LGS-LMN Wild *HS*	r^2
M1	*-0.342+0.150MF*	0.091	*-135744.899+0.289MF+0.077D*	0.452
	(5.722) (0.075)		*(67068.884) (0.049) (0.038)*	
M2	*0.982+0.135F -0.050Fch*	0.168	*-5.292+0.223F*	0.317
	(5.263) (0.069) (0.020)		*(3.313)(0.045)*	
M3	*11.079*		*11.096*	
	(0.526)		*(0.598)*	
M3’	*11.079*		*11.096*	
	(0.526)		*(0.598)*	
M4	*11.079*		*11.096*	
	(0.526)		*(0.598)*	
M4’	*11.079*		*11.096*	
	(0.526)		*(0.598)*	
M5	*11.079*		*-5.394+0.225*α_{o3}	0.325
	(0.526)		*(3.271) (0.044)*	
M6	*11.079*		*-4.973+0.221*α_{o6}	0.308
	(0.526)		*(3.314)(0.045)*	
M7	*11.079*		*-4.337+0.210*α_{oTT}	0.317
	(0.526)		*(3.125) (0.042)*	
M8	*11.079*		*-5.292+0.223*β_o	0.317
	(0.526)		*(3.313)(0.045)*	

Table 13: Models selected by forward stepwise procedure for LMN-MCN data. Standard errors for regression coefficients are given in parentheses. See text for variables included in models M1 to M8.

For variables in model	Models selected LMN-MCN Hatchery *HS*	r^2	LMN-MCN Wild *HS*	r^2
M1	*-598009.795+0.165F+0.341D*	0.405	*21.272*	
	(117867.598) (0.069) (0.067)		*(0.611)*	
M2	*-598009.795+0.165F+0.341D*	0.405	*21.272*	
	(117867.598) (0.069) (0.067)		*(0.611)*	
M3	*-529430.116+0.302D*	0.319	*21.272*	
	(120832.231) (0.069)		*(0.611)*	
M3’	*-529430.116+0.302D*	0.319	*21.272*	
	(120832.231) (0.069)		*(0.611)*	
M4	*-529430.116+0.302D*	0.319	*21.272*	
	(120832.231) (0.069)		*(0.611)*	
M4’	*-529430.116+0.302D*	0.319	*21.272*	
	(120832.231) (0.069)		*(0.611)*	
M5	$-608178.693+0.191\alpha_{o3}+0.346D$	0.429	*21.272*	
	(115607.112) (0.069) (0.065)		*(0.611)*	
M6	$-626393.142+0.204\alpha_{o6}+0.357D$	0.445	*21.272*	
	(115070.412) (0.068) (0.066)		*(0.611)*	
M7	$-623341.823+0.216\alpha_{oTT}+0.355D$	0.452	*21.272*	
	(113767.920) (0.069) (0.065)		*(0.611)*	
M8	$-598008.518+0.165\beta_{o}+0.341D$	0.405	*21.272*	
	(117867.583) (0.069) (0.067)		*(0.611)*	

Figures 10-12 were designed to visually compare the relative goodness-of-fit of the combinations of variables selected through stepwise regression. These figures plot the value of *HS* predicted by each submodel against the observed *HS*. The diagonal line corresponds to the equality E(*HS*) = *HS*, and the horizontal line is the weighted average of *HS*. The closer the model predictions are to the diagonal line, the better the fit is. Closeness to the horizontal line, on the contrary, suggests a poor improvement over the weighted average of *HS*.

In general, models containing predictors that measure flow at release day (*F*), the average flow level (*MF*) alone or combined with other variables (e.g., M1 and M2), as well as those containing the intercepts for predicted linear trends of flow over time (ao_3, ao_6, and ao_{TT}), sometimes combined with their corresponding slopes (e.g., M5, M6 and M7) presented somewhat acceptable fits. Their predicted *HS* values fell between the horizontal and diagonal lines (Figs. 10-14). However, the points are scattered loosely around the bisector line (Predicted *HS* = *HS*), which may suggest the need for some other predictors. In almost all the cases, the largest *HS* values were underestimated while the smallest ones were overestimated. The lack of fit of these extreme values of *HS* may have resulted from their extremely small sample sizes (N < 5 tagged fish).

For both LGR-LGS H and LGS-LMN H data, fits to model M2 (Tables 11-12), which contains the predictor *Fch*, were almost as good as fits to the competing model M1, which did not include this predictor (Fig. 10 and 12).

Models that included some measure of the linear trend of flow with respect to time (for example α_{13} in model M5, Table 11) fitted the LGR-LGS H data rather well (Fig. 10). Only predictions corresponding to *HS* greater than 15 km/day or smaller than 5 km/day were biased. But once again, these were predictions for release dates with small sample sizes (N < 5 fish). Thus, the observed *HS* may have been poorly estimated.

Finally, in the only occasion when *P5* was selected (M4' for LGR-LGS H, Table 11), the performance of the submodel was not better than that of competing models M5, M6 and M7 that

Figure 10: Predicted *HS* as function of *HS* for models selected by stepwise regression procedure for the LGR-LGS H subset. Horizontal line indicates the weighted average of *HS*; bisector line is equation "Predicted *HS* = *HS*". See Table 11 for model equations.

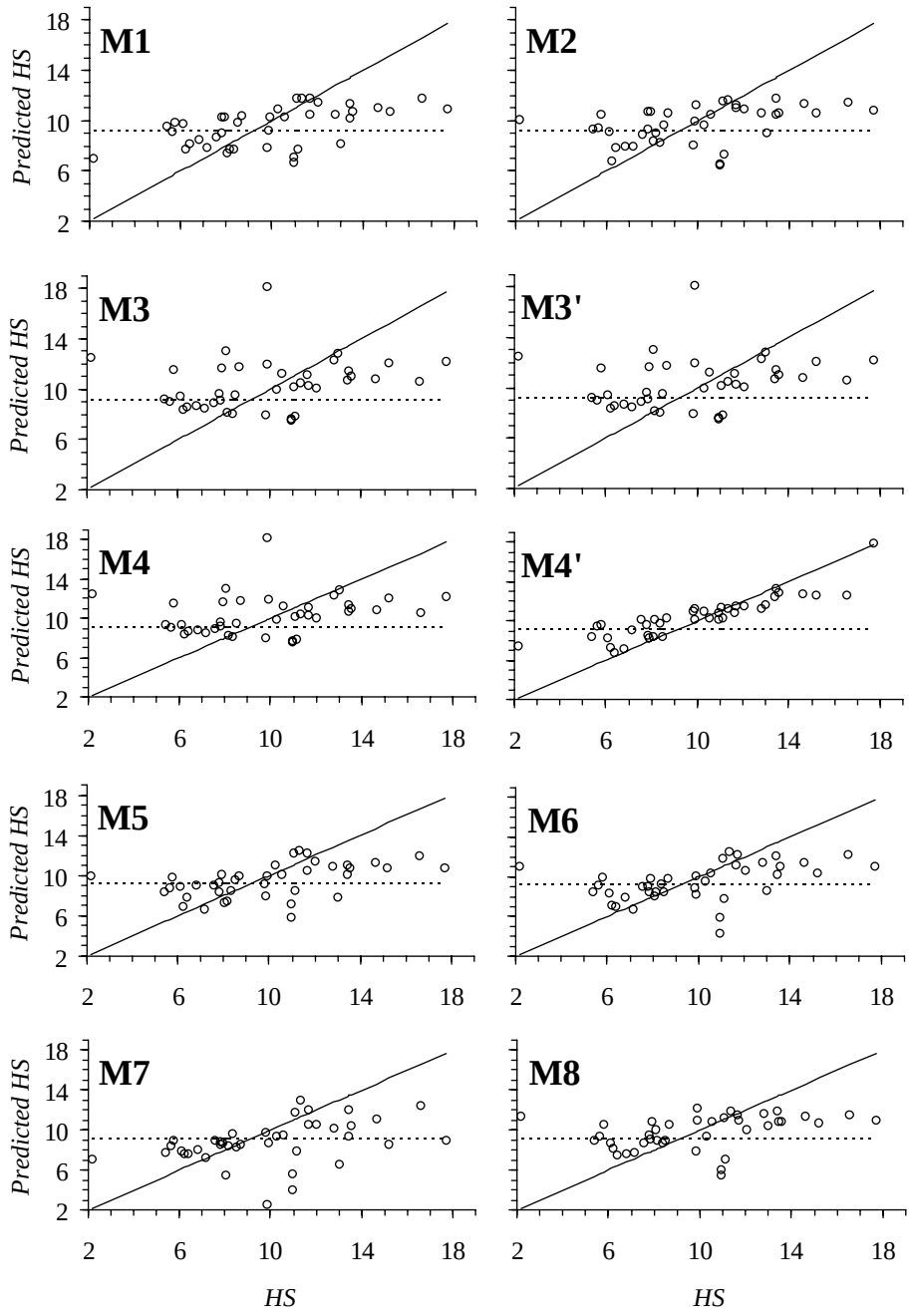


Figure 11: Predicted *HS* as function of *HS* for models selected by stepwise regression procedure for the LGR-LGS W subset. Horizontal line indicates the weighted average of *HS*; bisector line is equation "Predicted *HS* = *HS*". See Table 11 for model equations.

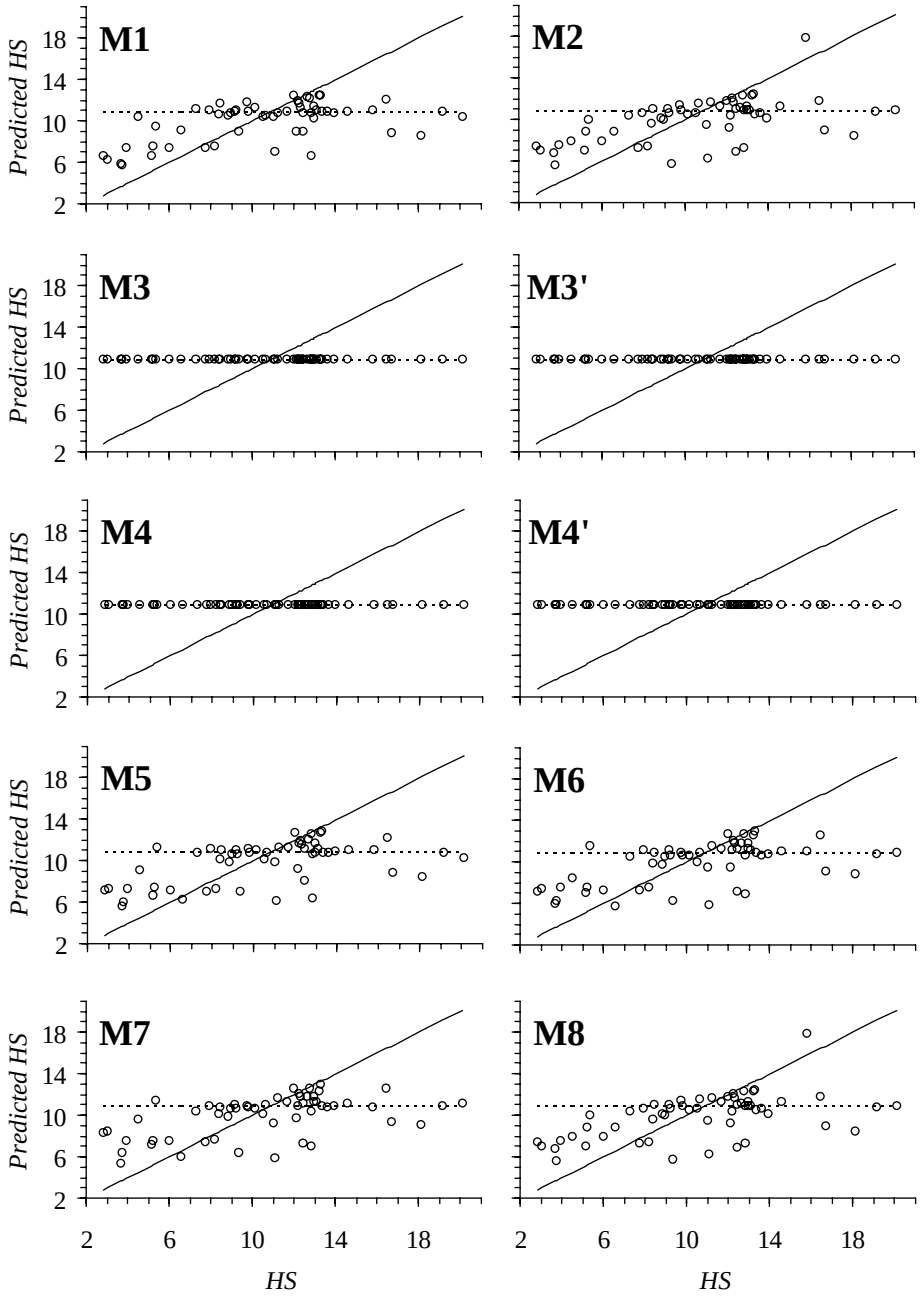


Figure 12: Predicted *HS* as function of *HS* for models selected by stepwise regression procedure for the LGS-LMN H subset. Horizontal line indicates the weighted average of *HS*; bisector line is equation "Predicted *HS* = *HS*". See Table 12 for model equations.

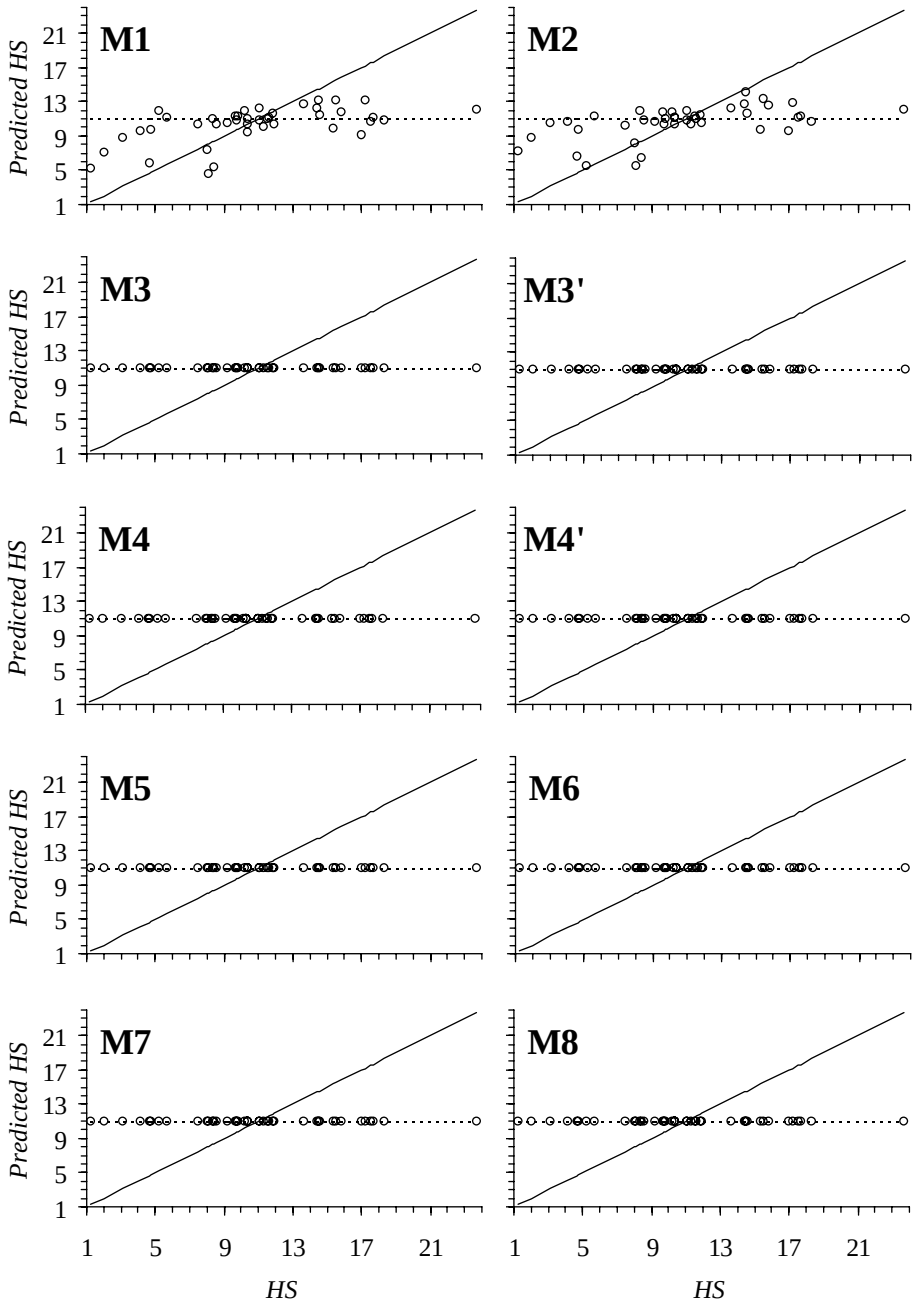


Figure 13: Predicted *HS* as function of *HS* for models selected by stepwise regression procedure for the LGS-LMN W subset. Horizontal line indicates the weighted average of *HS*; bisector line is equation "Predicted *HS* = *HS*". See Table 12 for model equations.

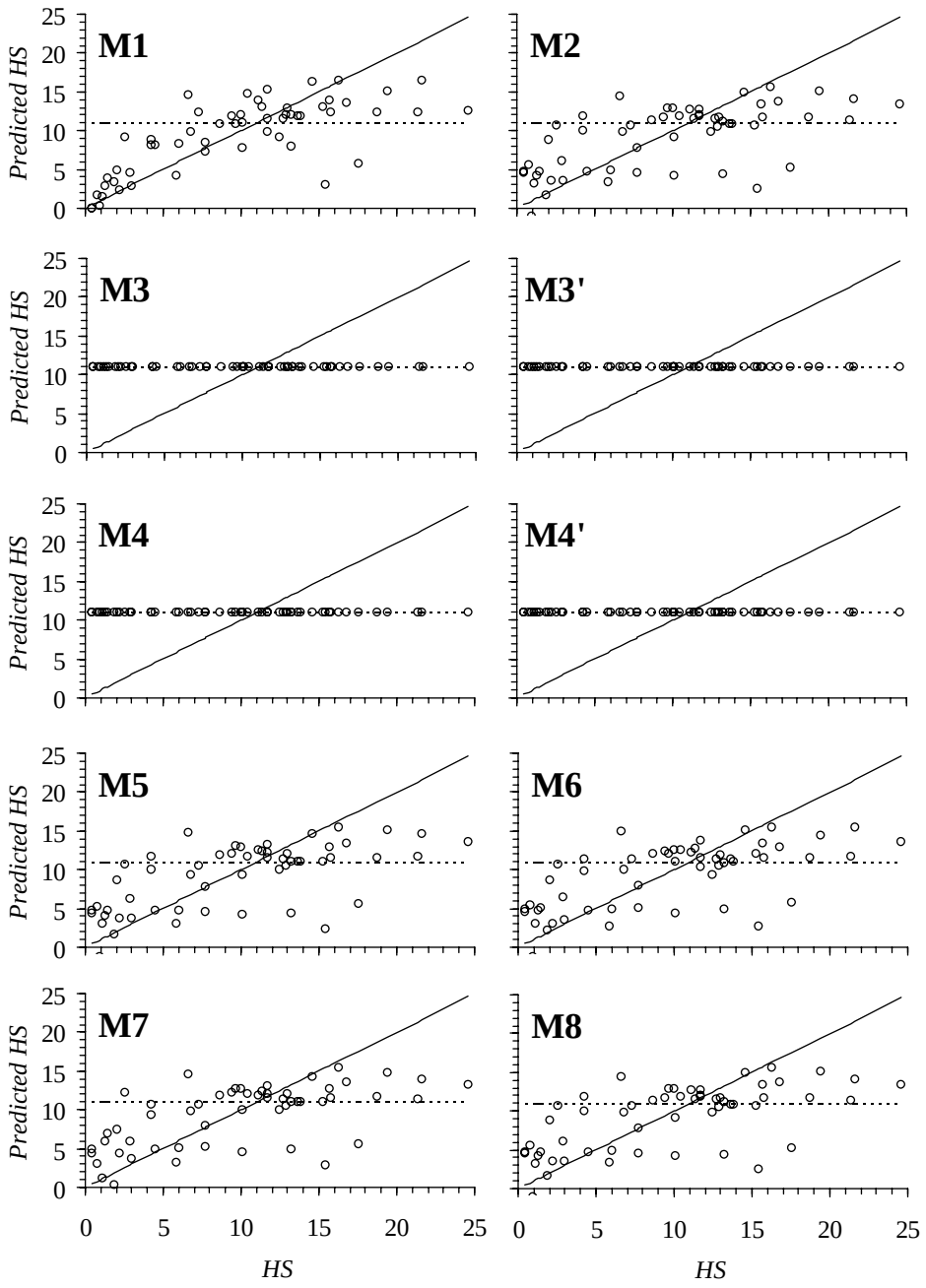


Figure 14: Predicted *HS* as function of *HS* for models selected by stepwise regression procedure for the LMN-MCN H subset. Horizontal line indicates the weighted average of *HS*; bisector line is equation "Predicted *HS* = *HS*". See Table 13 for model equations.

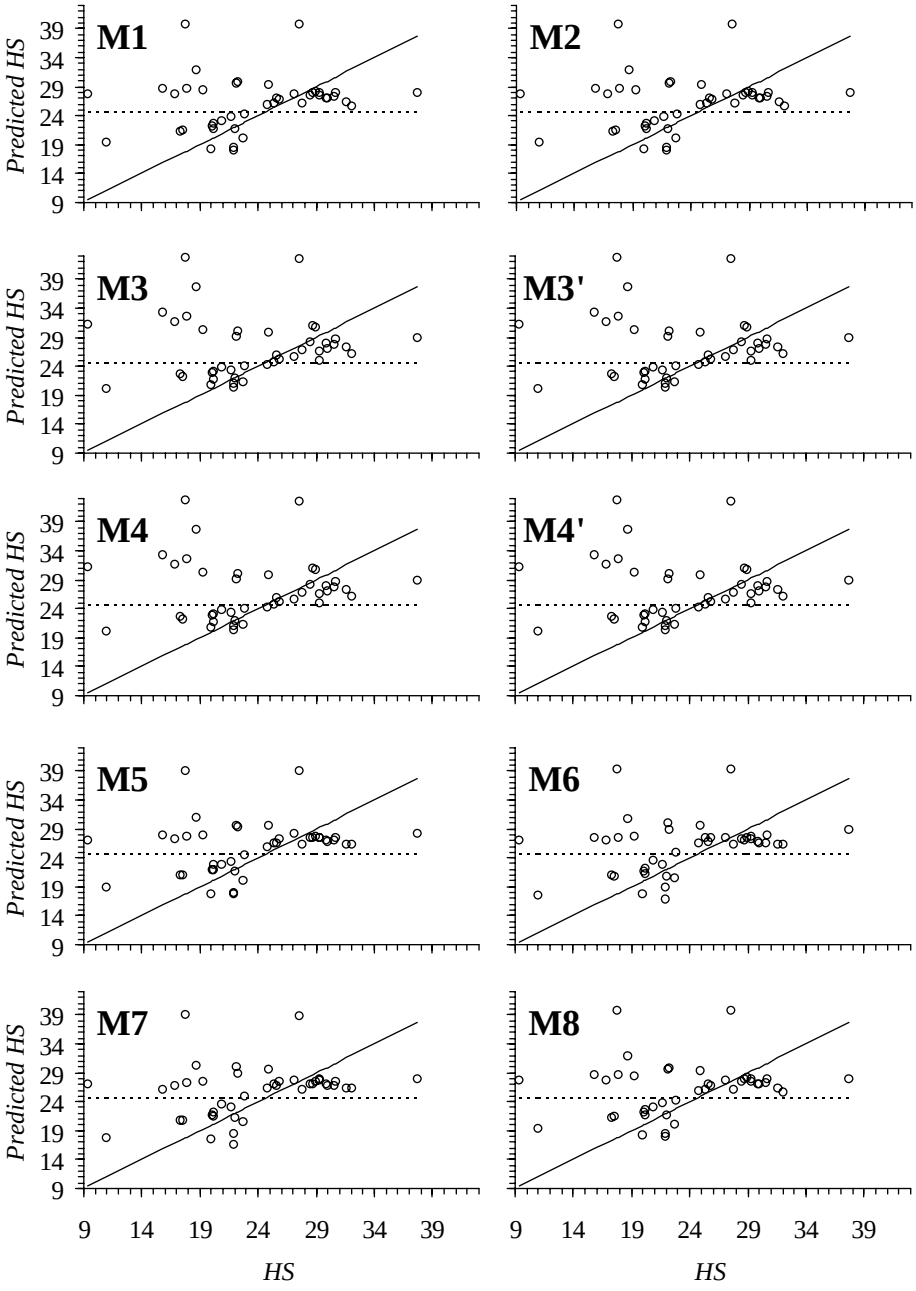
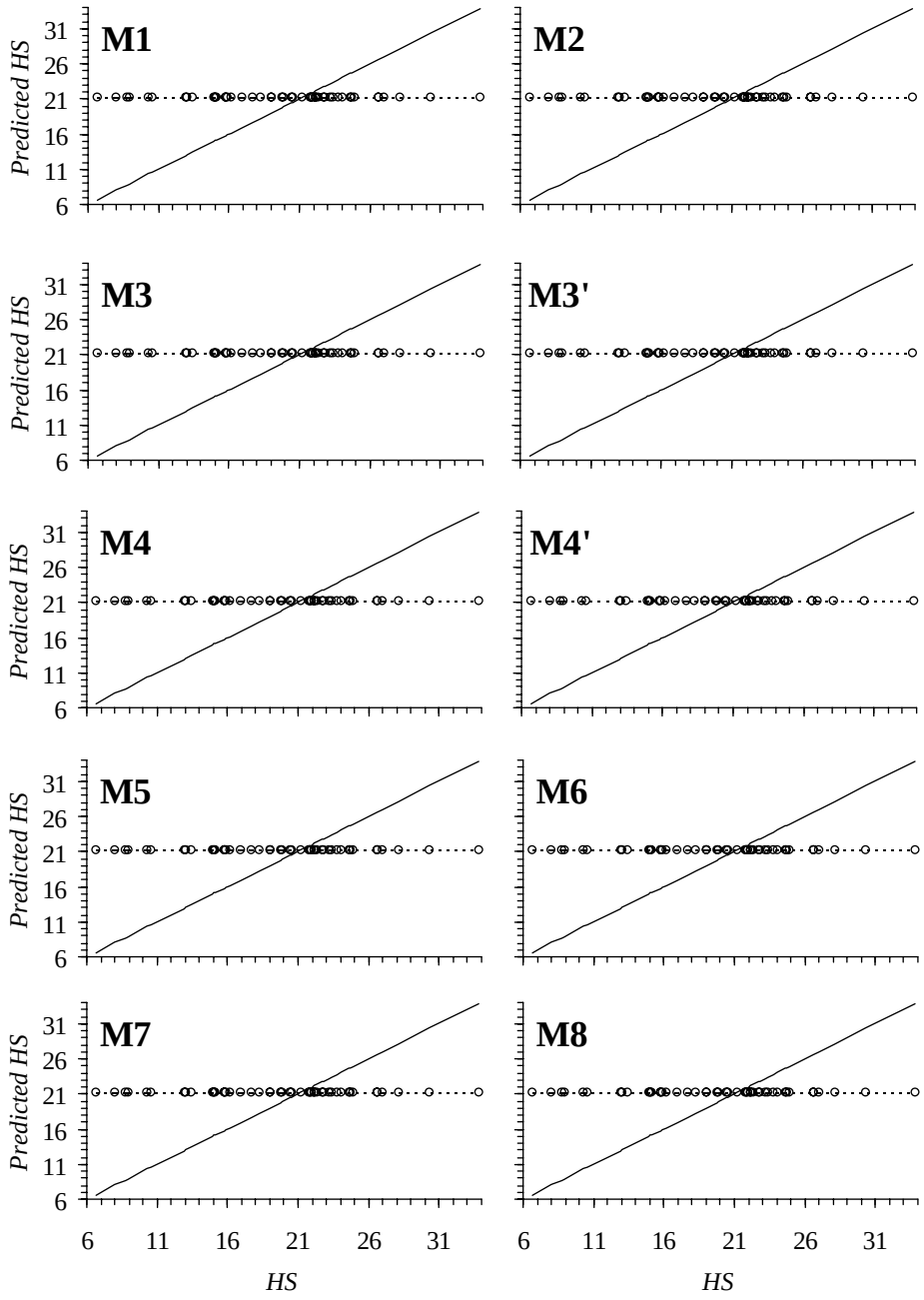


Figure 15: Predicted *HS* as function of *HS* for models selected by stepwise regression procedure for the LMN-MCN W subset. Horizontal line indicates the weighted average of *HS*; bisector line is equation "Predicted *HS* = *HS*". See Table 13 for model equations.



contained predictors that measure the linear trend of flow α_{13} or the intercepts of the regressions between flow and time α_{03}, α_{06}, and α_{0TT} (Fig. 10). Moreover, fits to model M4' were almost as good as those to models M1 and M2 that contained *MF*, and *F* and *Fch*, respectively.

4. DISCUSSION

The present study suggests (a) that there is some positive relationship between smolt migration speed and flow, and (b) that such relationship may be assessed in part by predictors such as the flow at release day, average flow during travel time, and some measure of the linear trend of flow during travel time. The study also points out to the difficulty in assessing any possible influence of pulses in river flow on travel speed.

Flow at release day *F* was positively correlated with *HS*, although inconsistently across subsets. Moreover, the intercepts of the regressions between flow and time (α_{03}, α_{06}, and α_{0TT}) and that of the polynomial regression (β_0), that may be interpreted as proxy for flow at release day were also positively correlated with *HS*. Thus, the flow at the start of the migration may be an important determinant of migration speed.

The average flow level during migration seems to contribute to migration speed, too, as suggested by the significant positive correlation between *MF* and *HS*. These results agree with previous findings (Zabel 1994) that showed that for certain cohorts of chinook and sockeyes smolts, the average flow conditions during migration help to improve estimates of migration rates in simple travel time models. Similarly, measures of linear trends of flow with time, for example our predictor variable α_{13}, were sometimes acceptable explanatory variables, in particular when the linear trend was measured over short portions of the migration period. These predictors, however, measured major characteristics of the flow pattern and could not explain all the variability in our response variable *HS*.

The importance of oscillations of different amplitude and frequency or pulses superimposed on the major temporal trend of flow (Figs. 7, 8, and 9) may affect migration speed.

For example, the simple predictor *FVAR* was negatively correlated with *HS* (Tables 2 to 7), suggesting that larger fluctuations of flow during migration may decrease the average fish speed. However, the variables designed to measure the effect of the day-to-day flow fluctuations, e.g., *P3c*, *P5c*, *P3* and *P5*, did not perform well as predictors of *HS*. Given that these predictors were calculated over periods of different duration and in two different ways (centered or not-centered), we argue that if there is any effect of pulsing, it cannot be captured by the simple orthogonal contrast formulae. In future studies, new predictor variables will have to be developed, and given the complexity of flow patterns, time series analysis techniques (e.g., spectral analysis) may be required.

Finally, our results were inconsistent between datasets, probably because the number of fish per release date varied substantially, increasing the variability of *HS* and thus affecting the ability of *HS* to show speed responses to flow changes. In future studies, it would be desirable to regulate the number of fish per release date by carefully planned releases of large number of smolts during periods when flow will display a particular pattern whose effect on travel time we may want to assess. Alternatively, other analytical approaches may be considered. For example, the distribution of travel times for each reach may be studied without separating the data by release day. The number of fish that cruise the reach in x days could be modeled as a multinomial distribution for which the probability parameters p's can be express as function of the average flow during travel time, the average linear trend of the flow, and any other characterization of flow fluctuation during travel time. The parameters of this function may then be estimated by maximizing the likelihood function. Alternatively, Zabel's (1994) two-parameter travel time model can be extended to incorporate not only the average flow condition, release dates, and individual fish length, but also new measures of flow pulses. Moreover, both parametric and nonparametric procedures normally used in the analysis of survival data in medical research (e.g., Collett 1994) could be used to analyze the travel time data. The *Hazard functions* (in this case, the probability that a fish arrives to a given dam at time t, conditional on it having traveled to that time) could be modeled in relation to flow-related variables.

5. REFERENCES

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