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# Migratory characteristics of juvenile ocean-type chinook salmon, *Oncorhynchus tshawytscha*, in John Day Reservoir on the Columbia River

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Both stream-type and ocean-type chinook salmon, *Oncorhynchus tshawytscha*, are found in the Columbia River system. Ocean-type chinook salmon migrate seaward and enter seawater as subyearlings or zero-age juveniles within a year of emergence, whereas stream-type fish reside in fresh water at least one full year before migrating (Healey, 1991). Yearling stream-type chinook salmon migrate through the mainstem Columbia River and its largest tributary, the Snake River, during the spring months (Raymond, 1979). In contrast, zero-age ocean-type chinook salmon migrate during the summer, but their migration can extend into autumn. Information regarding the migratory behavior of ocean-type chinook salmon in the impounded reaches of the Columbia River is limited. Early research showed that even during high-flow years, large numbers of zero-age ocean-type chinook salmon remained in John Day Reservoir on the Columbia River for a protracted time compared with stream-type chinook salmon (Raymond et al.<sup>1</sup>; Sims et al.<sup>2</sup>).

Hydroelectric development has been identified as an important factor that has contributed to decreased salmon and steelhead (*Oncorhynchus* spp.) production in the Columbia River Basin (Raymond, 1979, 1988; Williams, 1989). Direct mortality of downstream migrant juvenile salmonids is associated with passage through the turbines, spillways, and juvenile bypass systems at dams. Apart from direct mortality, a number of studies have indicated that the creation of impoundments, altered flows resulting from electric power demand, and irrigation withdrawals as a result of dam construction have slowed the seaward migration of juvenile salmonids (Raymond, 1969, 1979; Ebel and Raymond, 1976).

In an effort to lessen deleterious effects associated with hydroelectric dam construction, fisheries managers have developed water management strategies to augment instream flows to provide improved passage conditions for juvenile salmonids during their seaward migration (Northwest Power Planning Council, 1987). Rationale sup-

porting these actions is based largely on data by Sims and Ossiander<sup>3</sup> which described the migratory characteristics of juvenile stream-type chinook salmon and steelhead, *O. mykiss*, within the Snake River and in portions of the Columbia River. They found that increased instream flow volumes during the spring reduced smolt travel time through the hydroelectric complex and increased smolt survival. Similar data for ocean-type chinook salmon that migrate during the summer as zero-age juveniles are not available.

Berggren and Filardo (1993) suggested that increased water velocity increased migration speed for ocean-type chinook salmon and led to increased survival by reducing exposure time to predatory fish and to increasing summer water temperatures. There is ample evidence that predatory fish, principally northern squawfish, *Ptychocheilus oregonensis*, are abundant and consume large numbers of juvenile salmonids particularly during the summer in John Day Reservoir (Rieman et al., 1991; Vigg et al., 1991). However, the relationships between flows, migration rate, and survival are uncertain.

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<sup>1</sup> Raymond, H. L., C. W. Sims, R. C. Johnsen, and W. W. Bentley. 1975. Effects of power peaking operations on juvenile salmon and steelhead trout migrations, 1974. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to U.S. Army Corps of Engineers, 46 p.

<sup>2</sup> Sims, C. W., R. C. Johnsen, and W. W. Bentley. 1976. Effects of power peaking operations on juvenile salmon and steelhead trout migrations, 1975. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to U.S. Army Corps of Engineers, 36 p.

<sup>3</sup> Sims, C. W., and F. J. Ossiander. 1981. Migrations of juvenile chinook salmon and steelhead trout in the Snake River from 1973 to 1979: a research summary. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to U.S. Army Corps of Engineers, 31 p.

Developing water management strategies to benefit the juvenile stages of ocean-type chinook salmon has become an important issue in the Pacific Northwest; however, basic information describing migratory characteristics is required before such strategies can be designed. We undertook the present investigation to describe the migratory characteristics of ocean-type chinook salmon in John Day Reservoir, a major impoundment on the Columbia River. This paper describes the movement and residence time of zero-age ocean-type chinook salmon within the reservoir and examines the relationship between migration time through the reservoir and key environmental variables.

## Study area

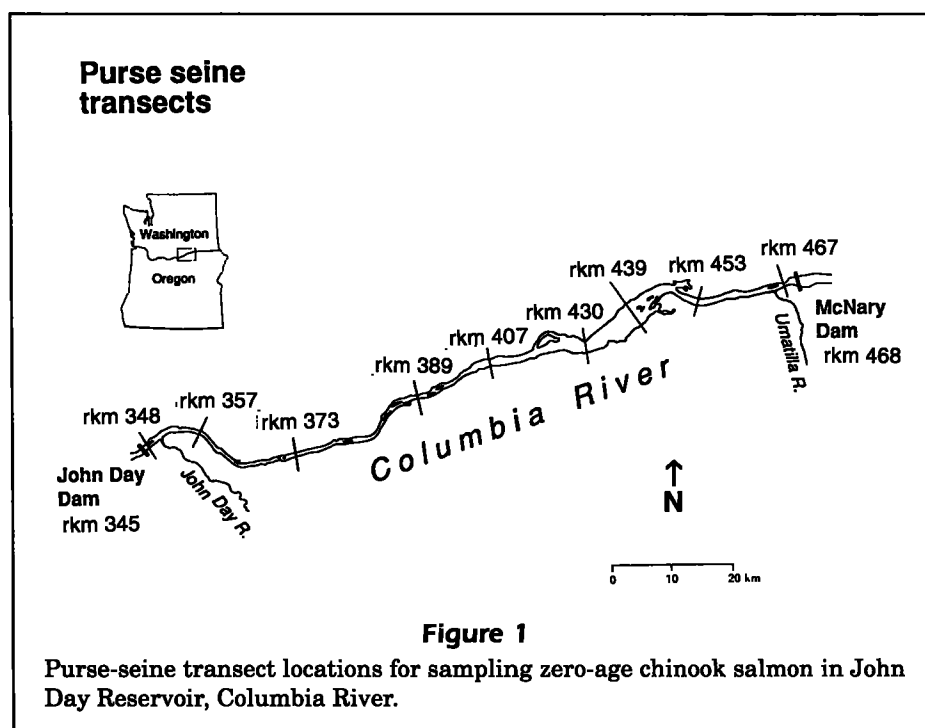
John Day Dam is a hydroelectric project on the Columbia River at river kilometer (rkm) 345, approximately 200 km east of Portland, Oregon (Fig. 1). The project was constructed and is operated by the U.S. Army Corps of Engineers (COE). The John Day Reservoir is the largest impoundment on the river, extending 122 km upstream to the tailrace of McNary Dam, located approximately 52 km downstream from the confluence of the Columbia and Snake rivers. The width of the reservoir ranges from 0.8 to 4.2 km, and its mid-pool depth extends to 48 m. The dam is ap-

proximately 1 km in length and is currently fitted with 16 turbines.

## Methods

Migrant zero-age chinook salmon entering the juvenile fish sampling facilities at McNary Dam were collected from mid-June through August 1981 through 1983. The fish were predominantly a mixture of fall and summer races (named for the time of adult returns) from the Columbia River and some small portion of fall races from the Snake River. The yearling chinook migration peaks during May at McNary Dam but can extend from April into June (FPC<sup>4</sup>). By mid-June more than 95% of the yearlings have passed the dam. During late June some yearlings remain mixed with the zero-age migrants. To minimize the inclusion of the larger yearlings in our experimental groups we used fish less than 110-mm fork length during June. Each week, up to three groups of fish were freeze branded with a unique mark (Mighell, 1969). All fish bearing the same brand were released into the tailrace below McNary Dam at 2100 h on their respective release dates to continue their downstream migration.

<sup>4</sup> Fish Passage Center. 1992. Fish Passage Center 1991 Annual Report. Columbia Basin Fish and Wildlife Authority, Portland, OR, 52 p.



Some of the freeze-branded fish were subsequently recovered downstream at John Day Dam. An airlift pump (Sims et al.<sup>5</sup>) was used to extract fish from the gatewells at Turbine Unit 3; however, it was unknown what proportion of recovered fish represented those passing into the turbine intake. Reliable estimates of that proportion are not available. Each day, collected fish were examined and brands enumerated. To provide a relative measure of daily passage at John Day Dam, the daily catch was expanded in proportion to the daily total river flow that was discharged through the sampled turbine unit. That proportion varied with prevailing spill volumes and the number of turbine units that were operating. Some water was also discharged through the navigation locks and fish ladders, but the amount was small, typically less than 1% of the total river discharge (Sims et al.<sup>6</sup>). The expanded daily catch was referred to as the passage index and was a relative measure of the number of fish passing the entire dam. The calculation of the passage index assumed 1) that the proportion of fish passing the dam through the spillway was equal to the proportion of water spilled, and 2) that the proportion of fish entering the gatewells from the turbine intake was relatively constant.

For each branded group, we constructed a distribution of daily passage indices. The median migration time for each group was estimated as the elapsed time between the known release date at McNary Dam and the date of median passage index distribution at John Day Dam. In addition, we estimated the passage index for the entire population passing John Day Dam each week.

Additionally, to characterize the movement patterns within John Day Reservoir, we freeze-branded, released, and subsequently recaptured zero-age chinook salmon at fixed cross-sectional transects located along the length of the reservoir (Fig. 1). We sampled fish with a 305 × 11 m purse seine (12-mm stretched mesh, knotless web throughout) aboard an 11-m power-block seiner. At each transect, a seine set was made as close to each shore as possible, allowing a minimum depth of 5 m for the seiner; the skiff would extend the net toward shore. A third set was executed at midreservoir. Sampling continued

throughout the summer and autumn until late November each year. Sampling extended from the forebay at John Day Dam (rkm 348) to the McNary Dam tailrace (rkm 467). We initially established and sampled nine transects spanning the length of the reservoir (Fig. 1). However, catches were so small at the three locations farthest upstream that we discontinued sampling those sites halfway through the 1981 sampling period. We cycled through all transects approximately every other week. All fish were anesthetized with MS-222, counted, and examined for marks. Unmarked fish were freeze branded, a subsample was measured for fork length, and after processing, all fish were allowed to recover from the anesthetic and were released.

To examine the effects of several key variables on migration rate from McNary to John Day Dam, we used correlation and regression techniques, analyzing each year separately and pooled together. The dependent variable was the median migration time (travel time) for each release group. The independent variables included release date, water temperature, and inverse river-flow volume. We used the inverse of volume, based on the hypothesis that fish would most likely respond to water velocity (water velocity is the river-flow volume divided by the cross-sectional area) and that fish travel time is related to water particle travel time, which is functionally inversely related to water velocity. Water temperature and flow were represented by a daily average over the 10-day period following the release date of each marked group. Water temperature and flow data were acquired from the COE. All data were originally reported by Giorgi et al.<sup>7</sup>

## Results

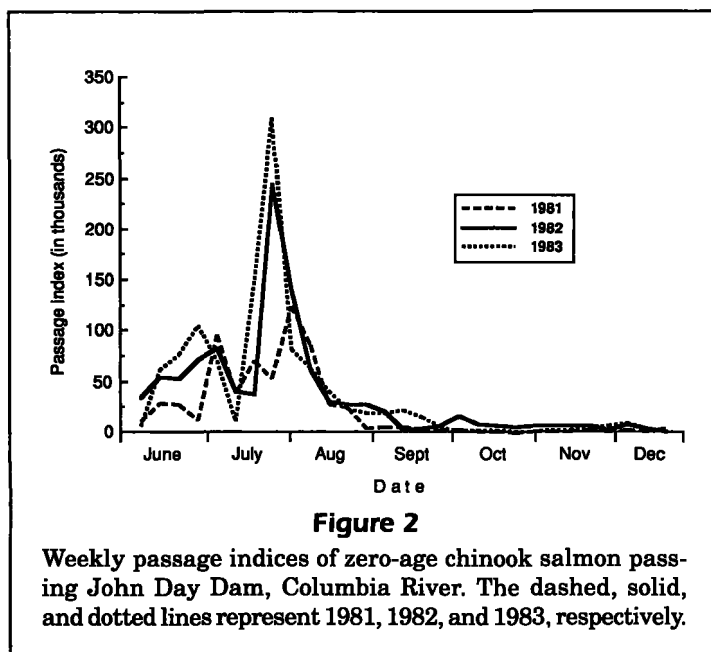
### Migration timing and migrant size

Each year, there was a minor peak in abundance of zero-age chinook salmon passing McNary Dam near the beginning of July and a major peak at the end of July (Fig. 2). In 1982 and 1983, the migration times for the zero-age chinook salmon populations passing John Day Dam were nearly identical. In 1982, 90% of the outmigrants had passed John Day Dam by the week ending 4 September and in 1983, by 26 August. In 1981, the passage distribution was somewhat dissimilar to those of 1982 and 1983; however, the 90th percentile of passage occurred during the week end-

<sup>5</sup> Sims, C. W., J. G. Williams, D. A. Faurot, R. C. Johnsen, and D. A. Brege. 1981. Migrational characteristics of juvenile salmon and steelhead in the Columbia River Basin and related passage research at John Day Dam, Vols. I and II. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to U.S. Army Corps of Engineers, 61 p.

<sup>6</sup> Sims, C. W., A. E. Giorgi, R. C. Johnsen, and D. A. Brege. 1983. Migrational characteristics of juvenile salmon and steelhead in the Columbia River Basin — 1982. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to U.S. Army Corp of Engineers, 35 p.

<sup>7</sup> Giorgi, A. E., D. R. Miller, and B. P. Sandford. 1990. Migratory behavior and adult contribution of summer outmigrating subyearling chinook salmon in John Day Reservoir. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to Bonneville Power Administration, 68 p.



ing 22 August, the same general time frame as in the following years.

Migrant size increased steadily over the course of the sampling period in all years. The mean size ranged from approximately 90 mm in early June to near 145 mm by the end of August. By mid-December, the length of fish passing John Day Dam aver-

aged approximately 170 mm. The smallest migrants observed passing either McNary or John Day Dam were 55 to 60 mm during the month of June each year. The largest migrants approached 225 mm in December. The fish sampled at all three sites (McNary Dam, John Day Dam, and within the reservoir) displayed the same size distributions during the sampling periods.

### Environmental conditions

Each year the trend in river flow was similar: discharge consistently decreased during the summer. However, the absolute flow volumes varied considerably over the three years of study (Tables 1–3). The greatest differences in flow volumes were observed each year from mid-June to mid-July. Beyond that period, flow volumes were nearly the same from year to year. The highest flow year occurred in 1982 when discharge levels averaged up to  $11.11 \times 10^3$  cubic meters per second during the last week of June. Overall, the lowest flows occurred in 1983. For example, during the last week of June, river discharge volumes were nearly half the maximum level observed in 1982, averaging between  $5.91 \times 10^3$  and  $6.87 \times 10^3$  cubic meters per second.

Water temperatures were similar among years and displayed the same tendency to increase throughout the summer (Tables 1–3). Early in the summer, water

**Table 1**

Summary of 1981 brand release and recovery data from groups of zero-age chinook salmon marked and released at McNary Dam and recaptured at John Day Dam. Travel time is the number of days required to traverse the reservoir from McNary Dam tailrace to John Day Dam. The percentiles were calculated from the passage indices.

Release date	Number of fish			Flow <sup>2</sup> m <sup>3</sup> ·sec <sup>-1</sup> (×10 <sup>3</sup> )	Temperature <sup>2</sup> (°C)	Travel time (days)		
	Released	Recovered	Passage index <sup>1</sup>			10	Percentiles 50	90
6/15	3,325	28	437	9.76	15	16	18	23
6/18	4,654	44	667	9.25	15	14	16	26
6/24	3,458	37	554	7.49	16	2	10	26
6/29	6,286	38	591	7.16	16	5	7	17
7/10	10,115	79	840	6.36	16	10	19	33
7/16	10,143	65	628	5.94	17	13	21	37
7/22	10,012	50	526	5.66	18	5	14	22
7/29	12,310	64	624	5.43	19	7	9	50
8/03	2,512	11	105	5.06	19	5	6	18
8/10	2,663	15	113	4.66	19	11	17	98
8/13	2,545	12	81	4.33	20	8	26	126
8/17	2,547	10	63	4.13	21	4	18	24
8/20	2,536	22	145	3.87	21	7	19	81
8/26	1,577	6	35	3.56	21	5	13	33

<sup>1</sup> The passage index is calculated daily as the ratio of the number recovered to the sampling effort and summed over days. Sampling effort was the average proportion of the total river flow discharged through Turbine Unit 3 during the 10-hour period 2000–0600 h.

<sup>2</sup> The average river-flow volume and water temperature over the 10-day period following release of the marked group.

Table 2

Summary of 1982 brand release and recovery data from groups of zero-age chinook salmon marked and released at McNary Dam and recaptured at John Day Dam. Travel time is the number of days required to traverse the reservoir from McNary Dam tailrace to John Day Dam. The percentiles were calculated from the passage indices.

Release date	Number of fish			Flow <sup>2</sup> m <sup>3</sup> ·sec <sup>-1</sup> (×10 <sup>3</sup> )	Temperature <sup>2</sup> (°C)	Travel time (days)		
	Released	Recovered	Passage index <sup>1</sup>			10	Percentiles 50	90
6/24	2,396	7	148	11.11	16	6	9	46
6/26	3,235	17	346	10.92	16	5	13	27
6/29	2,690	9	136	10.44	16	12	22	92
7/13	3,035	15	181	6.96	18	3	16	87
7/15	4,323	13	143	6.42	18	7	18	78
7/17	4,012	17	219	6.82	18	6	13	25
7/20	5,001	16	172	5.80	19	7	17	71
7/22	2,012	19	168	5.54	18	14	31	78
7/27	3,262	33	299	5.46	20	8	19	59
7/29	4,500	44	368	5.43	20	8	24	71
8/03	1,007	7	63	5.37	20	5	34	90
8/05	2,383	29	253	5.10	20	7	24	78
8/10	3,000	32	259	4.52	20	5	12	76
8/13	2,571	31	247	4.16	20	9	46	68
8/17	3,450	46	321	4.02	20	12	41	76
8/20	3,005	31	231	3.39	21	7	39	62
8/24	1,467	22	160	3.34	21	6	35	59
8/27	3,581	35	246	3.17	21	12	31	46
8/31	1,589	16	133	3.70	21	9	23	59
9/03	4,541	16	125	3.79	20	9	45	98

<sup>1</sup> The passage index is calculated daily as the ratio of the number recovered to the sampling effort and summed over days. Sampling effort was the average proportion of the total river flow discharged through Turbine Unit 3 during the 10-hour period 2000–0600 h.

<sup>2</sup> The average river-flow volume and water temperature over the 10-day period following release of the marked group.

Table 3

Summary of 1983 brand release and recovery data from groups of zero-age chinook salmon marked and released at McNary Dam and recaptured at John Day Dam. Travel time is the number of days required to traverse the reservoir from McNary Dam tailrace to John Day Dam. The percentiles were calculated from the passage indices.

Release date	Number of fish			Flow <sup>2</sup> m <sup>3</sup> ·sec <sup>-1</sup> (×10 <sup>3</sup> )	Temperature <sup>2</sup> (°C)	Travel time (days)		
	Released	Recovered	Passage index <sup>1</sup>			10	Percentiles 50	90
6/16	4,839	41	601	6.87	13	5	11	30
6/23	5,196	23	327	5.91	14	15	19	26
7/01	5,010	28	421	5.54	16	8	15	19
7/08	4,988	35	557	5.60	16	9	12	24
7/13	5,005	20	333	6.14	16	3	7	23
7/15	5,014	42	627	5.97	16	4	7	24
7/20	5,019	60	700	6.00	17	7	19	53
7/23	5,009	62	596	5.80	18	7	29	50
7/27	4,659	41	374	5.71	18	12	25	98
7/29	5,939	71	621	5.46	18	9	29	83
8/05	4,657	60	499	4.84	19	6	24	115
8/12	4,850	39	304	4.67	20	6	28	101
8/19	4,878	47	363	4.10	21	4	23	73
8/26	5,641	54	417	3.59	19	5	15	84
9/02	1,855	17	127	3.40	18	6	9	59

<sup>1</sup> The passage index is calculated daily as the ratio of the number recovered to the sampling effort and summed over days. Sampling effort was the average proportion of the total river flow discharged through Turbine Unit 3 during the 10-hour period 2000–0600 h.

<sup>2</sup> The average river-flow volume and water temperature over the 10-day period following release of the marked group.

temperatures ranged from 13 to 16°C, then increased steadily during the summer and peaked near 21°C by the end of August. Overall, 1982 was characterized by slightly higher water temperatures than the other two years.

### Fish travel time from McNary Dam to John Day Dam

For the three study years, a total of 49 freeze-branded groups were released to estimate fish travel time through the reservoir. The number of fish released in each group ranged from 1,007 to 12,310 (Tables 1–3). The estimated median travel time through John Day Reservoir for freeze-branded groups ranged from 6 to 26 days in 1981, 9 to 46 days in 1982, and 7 to 29 days in 1983 (Tables 1–3). Overall, the estimated median travel times were longest in 1982.

All individual groups exhibited protracted passage distributions at John Day Dam. The elapsed time between the 10th and 90th percentile of the recapture distributions typically exceeded several weeks (Tables 1–3). The fastest moving fish, those represented by the 10th percentile, traversed the reservoir in 2 to 16 days. The slowest moving fish, those represented by the 90th percentile, took 17 to 126 days to migrate through the reservoir.

The linear regression analyses, treating each year separately and pooling all years, did not identify a single model that was applicable to all years. Transformation of predictor variables did not improve the model. In fact, for each year, different sets of variables were included in the model constructed by the stepwise procedure. In 1981, the variability in travel time could not be explained by any predictor (Table 4), and none of the predictor variables entered the model. In 1982, only one predictor, release date, was entered into the model. In 1983, two variables, release date and water temperature, were entered

into the model. For the three years combined, only water temperature entered into the model. In all years, strong correlations were observed among the three predictor variables, with  $r$ -values ranging from 0.64 to 0.98.

### Intrareservoir movement

Upstream movement of fish after branding was regularly observed in the reservoir (Table 5). Detailed recapture histories for individual fish were reported in Sims and Miller,<sup>8</sup> and Miller and Sims.<sup>9,10</sup> In 1981, 1982, and 1983, the percentages of marked fish that were recaptured at or upstream from the transect of release were 67, 63, and 60%, respectively (Table 5). In each year, upstream movement was observed more frequently than stationary or downstream movement. Upstream movements were often pronounced, ranging from 9 to 82 km. Over the three years of study, the duration of the observed upstream movements ranged from 6 to 104 days. These observations indicated that the population at large was not consistently displaced downstream: rather, a large segment was engaged in pronounced upstream movement, or was stationary for extended periods.

<sup>8</sup> Sims, C. W., and D. R. Miller. 1982. Effects of flow on the migratory behavior and survival of juvenile fall and summer chinook salmon in John Day Reservoir. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to Bonneville Power Administration, 22 p.

<sup>9</sup> Miller, D. R., and C. W. Sims. 1983. Effects of flow on the migratory behavior and survival of juvenile fall and summer chinook salmon in John Day Reservoir. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to Bonneville Power Administration, 25 p.

<sup>10</sup> Miller, D. R., and C. W. Sims. 1984. Effects of flow on the migratory behavior and survival of juvenile fall and summer chinook salmon in John Day Reservoir. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to Bonneville Power Administration, 23 p.

**Table 4**

Regression models derived from stepwise multiple regression. The modelling procedure was applied to median zero-age chinook salmon travel times presented in Tables 1–3. Average water temperature, inverse average flow, and Julian release date were used in the model selection process.

Year	Model	$R^2$
1981	No variables were entered into the model	0.00
1982	Travel time = $-53.02 + 0.37$ (release date)	0.47
1983	Travel time = $-1.16 + 5.20$ (temperature) $-0.34$ (release date)	0.46
Combined	Travel time = $-22.83 + 2.36$ (temperature)	0.24

**Table 5**

Purse-seine recoveries of marked zero-age chinook salmon that were previously marked and released at various John Day Reservoir sampling transects, 1981–83.

	1981	1982	1983
Number of release groups	34	44	32
Number of fish released	14,273	13,126	22,206
Number of fish recaptured at transects in reservoir	63	41	111
Proportion recaptured at release site	0.11	0.12	0.16
upstream transects	0.56	0.51	0.44
downstream transects	0.33	0.37	0.40
Upstream recaptures			
excursion length; range (km)	10–80	16–82	9–82
excursion duration; range (d)	6–75	8–104	6–79

## Discussion

Our analyses indicated that no consistent set of predictors (water temperature, release date, or flow) could explain the travel time of zero-age ocean-type chinook salmon through John Day Reservoir. The predictors for travel time changed each year. The stepwise regression procedure failed to find any statistically significant variables to explain results in 1981, and flow was not a statistically significant predictor in any year. However, strong correlations among all predictor variables suggested that flow was nearly equally as likely a predictor as water temperature in 1983 and in the combined years, or as release date in 1982 and 1983.

Release date was included as a predictor variable to provide a generic measure to characterize time-based changes in fish development, such as size or physiological changes that progress over the course of the migration period. Since release date entered the model in two of the three years, this suggested that some time-based biological process may have been important. However, the strong correlations among predictor variables in each year limited the utility of such multivariable regression analyses for identifying the importance of any particular variable. Furthermore, in examining bivariate correlations we found no consistent relationships between migration time and any predictor variable.

Other measures of migratory behavior should be considered when characterizing the migratory dynamics of a population. One such measure we considered involved describing the directional intrareservoir movement of fish. We observed that within the body of the reservoir, zero-age ocean-type chinook salmon did not exhibit consistent downstream movement indicative of a continual, directed seaward migration. The majority of fish that were marked and released at transects throughout the reservoir were recaptured at or upstream from the site of release. This indicated that the population was not consistently displaced downstream passively via current. Based on laboratory observations of coho salmon, *O. kisutch*, Smith (1982) suggested that smolts in the Columbia River may be oriented mostly head-first upstream during outmigration, thus drifting downstream tail-first while being swept seaward. Our results indicate that zero-age chinook salmon do not fit this conceptual model.

The protracted reservoir-residence times apparent in our data are not necessarily peculiar to Columbia River stocks. Reimers (1973) studied fall chinook salmon in the Sixes River, Oregon, and suggested the optimum size at ocean entry is about 130 mm for that stock. He noted that this length was attained

by juveniles that remained in fresh or estuarine waters for extended periods of time, suggesting that extended freshwater residence is beneficial to zero-age fall chinook salmon. Extended residence of zero-age chinook salmon was observed in the Columbia River during the late 1950's (Mains and Smith, 1964), and even prior to dam construction (Rich, 1922).

The absence of a strong relationship between the migration rate and water velocity (flow) for ocean-type chinook salmon contrasts with evidence linking travel time to flow (Sims and Ossiander<sup>3</sup>; Sims et al.<sup>6</sup>), or developmental (smoltification) state, or both (Giorgi, 1990; Berggren and Filardo, 1993; Beeman et al.<sup>11</sup>) for migratory yearling stream-type chinook salmon.

The effects of smolt development on migratory behavior of zero-age fish are not clear. Zaugg (1982) cited a number of examples that suggested smolt development might be an important process governing migratory behavior of zero-age fall chinook salmon. In contrast, investigations conducted in the Rogue River, Oregon, indicated smolt development was not a requirement for downstream migration in ocean-type juveniles and its importance in affecting the rate of migration was not apparent (Ewing et al., 1980). Although the regression analysis in our investigation used a surrogate variable that may reflect smoltification-related effects (release date), its adequacy in representing such effects has not been verified. Future investigations should include direct assessments of effects associated with developmental processes, such as sodium and potassium ion levels and gill ATPase levels, as well as migrant size.

Berggren and Filardo (1993) also examined the relationship between travel time and a host of predictor variables for zero-age chinook salmon in John Day Reservoir. Their analysis included a subset of our data, as well as similar releases that were executed in 1986–88 (Harmon et al.<sup>12</sup>). In their multivariable approach, data were pooled across years. The variables in the final multiple regression model included release date, inverse flow, and an index of the absolute change in flow. The bivariate relationship between smolt travel time and inverse flow had an associated  $r^2$  value of 0.28. In contrast to our results, they concluded that increased flows reduced travel time of zero-age chinook salmon.

<sup>11</sup> Beeman, J. W., D. Rondorf, J. Falter, M. Free, and P. Haner. 1990. Assessment of smolt condition for travel time analysis. U.S. Fish Wild. Serv., Cook, WA 98605. Report to Bonneville Power Administration, 71 p.

<sup>12</sup> Harmon, J. R., G. M. Matthews, D. L. Park, and T. E. Ruehle. 1989. Evaluation of transportation of juvenile salmonids and related research on the Columbia and Snake Rivers, 1988. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to U.S. Army Corp of Engineers, 11 p.

The variability in travel-time estimates observed in this study may in part have resulted from limited sampling capability at John Day Dam, since only 0.3 to 1.3% of any marked group was recovered at that site. There were four groups from which less than 10 recaptures were observed (Tables 1 and 2). However, the travel-time estimates of Berggren and Filardo (1993) displayed generally the same range of values, even though sampling effort at John Day Dam was increased during the latter years on which their analyses were based.

Another confounding factor is that our investigation treated the entire composite population of zero-age juveniles. For future studies, we suggest studying individual stocks of fish to describe any unique migratory characteristics that may be stock-specific.

## Acknowledgments

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