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Migrational Behavior and Seaward Movement of Wild Subyearling Fall Chinook Salmon in the Snake River

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Abstract.—Flow augmentation increases flow and decreases temperature in reservoirs in the lower Snake River during the seaward migration of wild subyearling fall chinook salmon *Oncorhynchus tshawytscha*. A study of the migrational behavior and seaward movement of wild subyearling fall chinook salmon in the Snake River was necessary to help understand the efficacy of flow augmentation. We studied fall chinook salmon in the Snake River during 1992–2001. After analyzing mark–recapture data, we deduced that fall chinook salmon passed through at least four migrational phases, including (1) discontinuous downstream dispersal along the shorelines of the free-flowing river, (2) abrupt and mostly continuous downstream dispersal offshore in the free-flowing river, (3) passive, discontinuous downstream dispersal offshore in the first reservoir encountered en route to the sea, and (4) active and mostly continuous seaward migration. We used ordinary-least-squares multiple regression to test the effects of flow (m^3/s), temperature (°C), and three other factors on the rate of seaward movement (km/d) from initial tagging in the free-flowing river to the first dam encountered en route to the sea (period 1) and from passage at this first dam to passage at the next dam downstream (period 2). We found that flow and temperature influenced the rate of seaward movement during period 1 ($N = 2,808$; flow model $R^2 = 0.65$, $P \leq 0.0001$; temperature model $R^2 = 0.726$, $P \leq 0.0001$). We failed to find evidence for flow and temperature effects on the rate of seaward movement during period 2, possibly because of limitations on our study. We conclude that flow augmentation increases the rate of seaward movement of fall chinook salmon during period 1, provided that augmentation occurs when the fish have moved offshore in the free-flowing river and are behaviorally disposed to being displaced downstream. The cooling effect of summer flow augmentation likely prevents fish that successfully smolted during period 1 from reverting to parr during period 2, but research is needed to confirm this hypothesis.

The migrational behavior of juvenile chinook salmon *Oncorhynchus tshawytscha* varies within the species. Stream-type chinook salmon (Healey 1991) generally overwinter in their natal streams or larger-order streams as subyearlings, and then migrate seaward as yearling smolts the following spring (Chapman and Bjornn 1969; Bjornn 1971; Achord et al. 1996). Ocean-type chinook salmon typically begin seaward movement in the spring soon after fry emergence, and the smolts reach the sea as subyearlings (Healey 1991).

In the Snake River, wild ocean-type fall chinook salmon emerge from the gravel in the spring, parr grow rapidly, and smolts migrate seaward in late spring and summer (Connor et al. 2002; Connor and Burge, this issue). A small number of wild subyearling spring and summer chinook salmon disperse long distances from natal streams into the Snake River, where they adopt an ocean-type life history similar to that of fall chinook salmon (Connor et al. 2001a, 2001b). For simplicity, we refer to wild subyearling chinook salmon in the Snake River as fall chinook salmon.

To increase survival of fall chinook salmon passing downstream in reservoirs in the lower Snake River during the summer, water is released from Dworshak Reservoir and reservoirs upstream of Hells Canyon Dam (Figure 1). This water man-

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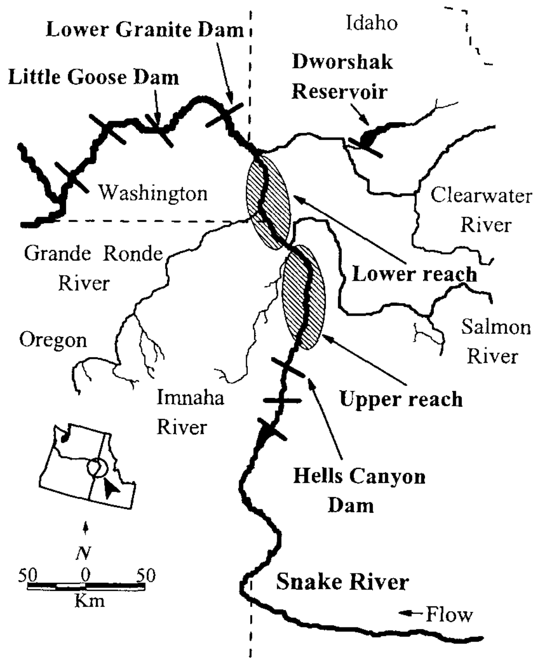

FIGURE 1.—Map of the Snake River showing the upper and lower reaches where juvenile fall chinook salmon were captured, tagged, and released to resume rearing and seaward movement, 1992–2001. The locations of Hells Canyon Dam, Lower Granite Dam, Little Goose Dam, and Dworshak Reservoir are also shown.

agement strategy is called summer flow augmentation, and it increases flow and decreases temperature in the lower Snake River reservoirs (Connor et al. 1998; Connor et al. 2003, this issue). For example, flow in Lower Granite Reservoir increased from approximately 600 to 1,250 m^3/s and temperature declined from 20°C to 17°C when summer flow was implemented in 1994 (Connor et al. 1998). The flow increase is intended to increase survival by increasing the rate of seaward movement, thereby reducing exposure time to predators and warm summer temperatures (NMFS 1995). The decrease in temperature is intended to increase fall chinook salmon survival by reducing predation and mortality associated with thermal stress (NMFS 1995).

Studies on the relation between the flow and rate of seaward movement of ocean-type chinook salmon have produced equivocal results. Berggren and Filardo (1993), Giorgi et al. (1997), and Tiffan et al. (2000) studied ocean-type chinook salmon passing downstream in Columbia River reservoirs. Berggren and Filardo (1993) concluded that seaward movement increased as flow increased, thus flow augmentation helps to mitigate dam-caused passage delays. Tiffan et al. (2000) concluded that flow was weakly related to seaward movement. Giorgi et al. (1997) concluded that there is no evidence for a relation between downstream migration rate and flow.

Temperature effects on the rate of seaward movement of ocean-type chinook salmon result primarily from the influence of temperature on growth and smoltification. Fall chinook salmon grow rapidly, exhibit normal physiological patterns of smolt development, and become progressively more migratory as temperature increases from approximately 9°C to 17°C (Banks et al. 1971; Boeuf 1993; Curet 1994; Marine 1997; Connor et al. 2002; Connor and Burge 2003). Thermal stress resulting from exposure to temperatures above 20°C can disrupt growth, metabolic activity, and the normal pattern of smoltification (Marine 1997; Mesa et al. 2002). Therefore, the rate of seaward movement likely decreases at some threshold temperature.

We conducted a study of juvenile Snake River fall chinook salmon from 1992 to 2001 to help fishery managers understand how flow and temperature influence migrational behavior and seaward movement. In this paper, we describe the migrational behavior of fall chinook salmon from the time of shoreline rearing in the free-flowing Snake River to the time of passage at two downstream dams. We also test the effects of flow, temperature, and three other factors on the rate of seaward movement.

Study Area

The Snake River can be divided into two reaches. The upper reach extends from Hells Canyon Dam to the Salmon River confluence, and the lower reach extends from the Salmon River confluence to the upper end of Lower Granite Reservoir (Figures 1, 2). The upper reach is warmer (winter–spring temperature, 8.4 ± 0.2°C [mean ± SE]) than the lower reach (winter–spring temperature, 7.9 ± 0.2°C) (Connor et al. 2002). The channel gradient (Figure 2) in the upper reach is higher than in the lower reach (upper reach, 1.4 m/km; lower reach, 0.6 m/km; Dauble and Geist 2000). The distribution of beach seining sites demonstrates differences in rearing habitat connectivity between the two reaches (Figure 2).

Methods

Data collection.—From 1992 to 2001, field personnel used a beach seine to capture juvenile fall

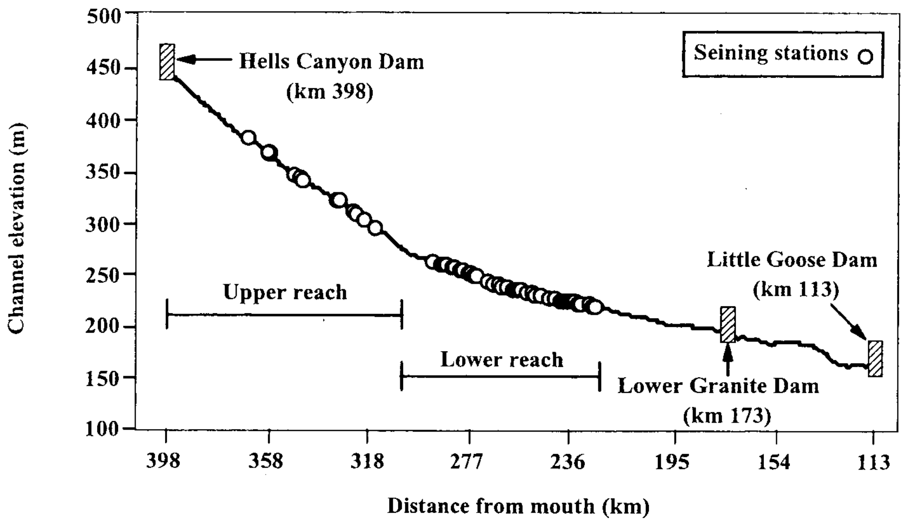

FIGURE 2.—Channel elevation profile of the Snake River from Hells Canyon Dam to Little Goose Dam (data from Dauble and Giest [2000]) and the locations of beach seining stations in the upper and lower reaches of the Snake River where juvenile fall chinook salmon were captured, tagged, and released, 1992–2001.

chinook salmon (Connor et al. 1998). Sampling typically started in April, soon after fry began emerging from the gravel. Sampling was conducted at permanent stations 1 d/week in the upper reach of the Snake River and 2 d/week in the lower reach. Supplemental sampling was conducted 1 or 2 d/week for three consecutive weeks at additional stations within each reach once the majority of fish were at least 60 mm in fork length (FL). Sampling was discontinued in June or July when the majority of fish had moved into Lower Granite Reservoir.

Passive integrated transponder (PIT) tags (Prentice et al. 1990a) were inserted into fall chinook salmon 60 mm FL and longer (Connor et al. 1998). Tagged fish were released at the collection site after a 15-min recovery period. Some of the tagged fish were recaptured during beach seining in the free-flowing river after initial capture, tagging, and release (hereafter, initial tagging). Some of the PIT-tagged fish were detected after they passed into the fish bypass systems of Lower Granite and Little Goose dams (Figures 1, 2). See Matthews et al. (1977) and Prentice et al. (1990b) for a description of fish bypass systems and PIT tag monitoring equipment.

Migrational behavior during shoreline rearing.—We pooled the data within each reach across years. We calculated the number of fall chinook salmon captured and mean fork length by month. During preliminary analyses, we made comparisons to ensure that supplemental sampling did not unduly bias these calculations. By reach, we calculated the distance traveled and the number of days that elapsed between the initial tagging and recapture of each PIT-tagged fish during beach seining. For PIT-tagged fish that were recaptured downstream of initial tagging sites, we calculate dispersal rate (km/d) as the distance traveled divided by the number of days that elapsed between the initial tagging and recapture.

Time in the river versus the reservoir.—We used data collected on PIT-tagged fall chinook salmon that were both recaptured by beach seine and detected passing Lower Granite Dam to estimate how many days fish spent in the free-flowing river and in Lower Granite Reservoir after initial tagging. For each recaptured fish, we used the number of days that elapsed between its initial tagging and recapture by beach seine as an estimate of the number of days spent in the river. Travel time to Lower Granite Dam was then calculated for each fish as the number of days that elapsed between initial tagging and detection at Lower Granite Dam. We used the difference between travel time and the estimated the number of days spent in the river as an estimate of the number of days spent in the reservoir. For example, if a fish was initially tagged on 1 May (day of year = 121 when 1 January = 1) and recaptured by beach seine on 10 May (day of year = 130) the estimated number of days spent in the river would be 9 d (= 130 − 121). If the detection date for this fish at Lower Granite Dam was 15 June (day of year = 166), its travel time would be 45 d (= 166 − 121), and the estimated number of days it spent in the reservoir would be 36 d (= 45 d − 9 d).

We estimated where PIT-tagged fall chinook salmon from each reach spent the majority of days in transit to Lower Granite Dam each year after initial tagging by comparing the least-squares mean number of days spent in the river with the least-squares mean number of days spent in the reservoir. We used a two-way (location [i.e., river and reservoir] × year) repeated-measures analysis of variance (ANOVA; Ott 1993) to make this comparison ($\alpha = 0.05$). We made pairwise comparisons ($\alpha = 0.05$) by use of Fisher's test for least significance difference (Ott 1993). Adequate numbers of fish were recaptured and then detected at Lower Granite Dam to run the ANOVA during 1995 and 1998–2000 in the upper reach and during 1993–1996 and 1998–2001 in the lower reach.

Rate of seaward movement by reach.—We calculated the rate of seaward movement for PIT-tagged fall chinook salmon passing downstream from initial tagging sites to Lower Granite Dam (hereafter, period 1) as the distance traveled to Lower Granite Dam (located 173 km from the Snake River mouth) divided by the travel time to Lower Granite Dam. We $\log_e$ transformed the rate of seaward movement to normalize the data and then used a two-way ANOVA on reach and year ($\alpha = 0.05$). We used Fisher's test for least significance difference to make pairwise comparisons ($\alpha = 0.05$). Data collected during 1995–2001 were used in the ANOVA because both reaches were sampled.

We calculated the rate of seaward movement for PIT-tagged fall chinook salmon passing downstream between Lower Granite and Little Goose dams (hereafter, period 2) as the distance between dams (60 km) divided by the travel time measured from detection at Lower Granite Dam to detection at Little Goose Dam. We $\log_e$ transformed the rate of seaward movement to normalize the data and then ran a two-way ANOVA as described for period 1. Data collected during 1996–2001 were used in the ANOVA because both reaches were sampled, and large numbers of fish were removed at Lower Granite Dam prior to 1996 (e.g., Connor et al. 2001a).

Rate of seaward movement by period.—We determined whether the rate of seaward movement of PIT-tagged fall chinook salmon increased between initial tagging and detection at Little Goose Dam by comparing the rates of seaward movement observed during periods 1 and 2. We used a two-way (period and year) repeated measures ANOVA and Fisher's test for least significance difference to make this comparison ($\alpha = 0.05$). We used data collected during 1996–2001 for the ANOVA. Period 2 data collected prior to 1996 were not analyzed because large numbers of PIT-tagged fall chinook salmon were removed at Lower Granite Dam as previously mentioned.

We used logistic regression (Johnson 1998) to determine whether the rate of seaward movement of a PIT-tagged fall chinook salmon during period 1 had any influence on its probability of surviving and being detected at Little Goose Dam. Finding such a relation would imply that a change in the mean rate of seaward movement between periods might be the result of the survival of inherently fast-migrating fish, as opposed to a change in migrational disposition as fish move downstream. Logistic regression models for period 1 rates of seaward movement from 1996 to 2001 were fitted separately by reach and year. We determined whether the rate of seaward movement during period 1 affected the probability of survival and detection at Little Goose Dam based on the accuracy (% correct classifications) of the logistic regression models.

Factors affecting rate of seaward movement during period 1.—We used ordinary-least-squares multiple regression (hereafter, regression) to describe the factors affecting the rate of seaward movement of PIT-tagged fall chinook salmon during period 1. We analyzed the following factors: (1) mean flow (m^3/s) measured by U.S. Army Corps of Engineers personnel at Lower Granite Dam between initial tagging of a PIT-tagged fall chinook salmon and its detection at Lower Granite Dam; (2) mean temperature (°C) measured by U.S. Army Corps of Engineers personnel in the forebay of Lower Granite Dam between initial tagging and detection at Lower Granite Dam; (3) initial tagging date (day of year); (4) fork length (mm) measured at initial tagging; and (5) riverine distance traveled (km) by a fish in the free-flowing Snake River before entering Lower Granite Reservoir.

We pooled the data across reaches and years (1992–2001) to increase the range of the factors (e.g., Berggren and Filardo 1993; Giorgi et al. 1997). We $\log_e$ transformed the rate of seaward movement to improve linearity and remedy heteroscedasticity of residuals, and then fit regression models from every possible combination of factors. We examined the slope coefficients (b) of each factor in every model for sign changes and for inflated standard errors (hence, failure to reject the null hypothesis H_o: $b = 0$). Sign changes and large standard errors are indications of problematic multicollinearity (Dielman 1996). We also built a Pearson's correlation matrix to examine the level of collinearity between each factor. Models with problematic multicollinearity or models that included factors with nonsignificant ($P > 0.05$) slope coefficients were removed from further analysis. Fit was compared among the remaining regression models based on the coefficient of determination (R^2). We report the three regression models that had the highest R^2 values.

We made residual plots for flow and temperature as described for flow in the following example. The $\log_e$ transformed rate of seaward movement was regressed against fork length and riverine distance. The residuals from this regression were then plotted against flow. A line was fitted to the residuals by regressing them against flow. The resulting residual plots provided a better graphical representation of the relation between flow and rate of seaward movement because the variability in the downstream migration rate attributable to fork length and riverine distance had been removed.

Factors affecting rate of seaward movement during period 2.—We used data collected during 1996–2001 for period 2 model fitting. Period 2 data collected prior to 1996 were not analyzed because large numbers of PIT-tagged fall chinook salmon were removed at Lower Granite Dam. We fitted regression models as described for period 1. The factors analyzed were (1) mean flow (m^3/s) in Little Goose Reservoir between detections at Lower Granite and Little Goose dams; (2) mean temperature (°C) in Little Goose Reservoir between detections at Lower Granite and Little Goose dams; (3) detection date (day of year) at Lower Granite Dam; (4) fork length (mm) at initial tagging in the Snake River; (5) total distance traveled (km) from initial tagging to detection at Little Goose Dam; and (6) travel time (d) between initial tagging and detection at Lower Granite Dam. We report the regression model that had the highest R^2.

Results

Migrational Behavior during Shoreline Rearing

A total of 8,536 fall chinook salmon were captured in the upper reach of the Snake River (years 1995–2001). A total of 24,149 fish were captured in the lower reach (years 1992–2001). Catch peaked when fork length averaged 61 and 56 mm in the upper and lower reaches, respectively (Table 1). The number of fish captured decreased from May to July as mean fork length increased to 92 mm in the upper reach and to 86 mm in the lower reach (Table 1).

TABLE 1.—Monthly sample sizes and mean fork lengths (FL mm; ± SD) of fall chinook salmon captured by beach seining in the upper (1995–2001) and lower (1992–2001) reaches of the Snake River.

	Upper reach		Lower reach	
Month	*N*	FL	*N*	FL
Apr	2,961	46 ± 6	2,492	46 ± 6
May	4,056	61 ± 13	12,336	56 ± 11
Jun	1,465	83 ± 12	8,808	73 ± 14
Jul	54	92 ± 15	513	86 ± 16

A total of 442 (15%) of the 2,862 PIT-tagged fall chinook salmon from the upper reach were recaptured during beach seining; 413 of these were recaptured at initial tagging locations from 5 to 35 d (median, 9 d) after initial tagging. A total of 1,201 (11% of 10,617 tagged) fish from the lower reach were recaptured, of which 1,094 were recaptured at initial tagging locations from 1 to 42 d (median, 7 d) after initial tagging.

Approximately 1% of the fall chinook salmon PIT-tagged in each reach of the Snake River (upper reach, $N = 29$; lower reach, $N = 107$) were recaptured downstream of initial tagging locations. The median distance traveled was 79 km (range, 4–126 km) for fish from the upper reach and 3 km (range, 1–43 km) for fish from the lower reach. Median dispersal rates were 5.5 km/d (range, 0.2–25.2 km/d) and 0.3 km/d (range, 0.1–31.0 km/d) for fish from the upper and lower reaches, respectively.

Time in the River versus the Reservoir

A total of 188 PIT-tagged fall chinook salmon from the upper reach of the Snake River were both recaptured by beach seine and detected passing Lower Granite Dam during 1995 and 1998–2000. The estimated annual mean number of days that these fish spent in the free-flowing Snake River after initial tagging ranged from 10 to 15 d, and the annual mean number of days spent in Lower Granite Reservoir ranged from 20 to 42 d (Figure 3). Results from two-way ANOVA showed that the interaction between location and year was significant ($F = 15.00$, $P < 0.0001$) but orderly, indicating the tests for main effects were appropriate. The main effects of location and year were significant (location, $F = 249.33$, $P < 0.0001$; year, $F = 12.14$, $P < 0.0001$). After initial tagging, the fish from the upper reach spent significantly ($P < 0.05$) fewer days in the river than in the

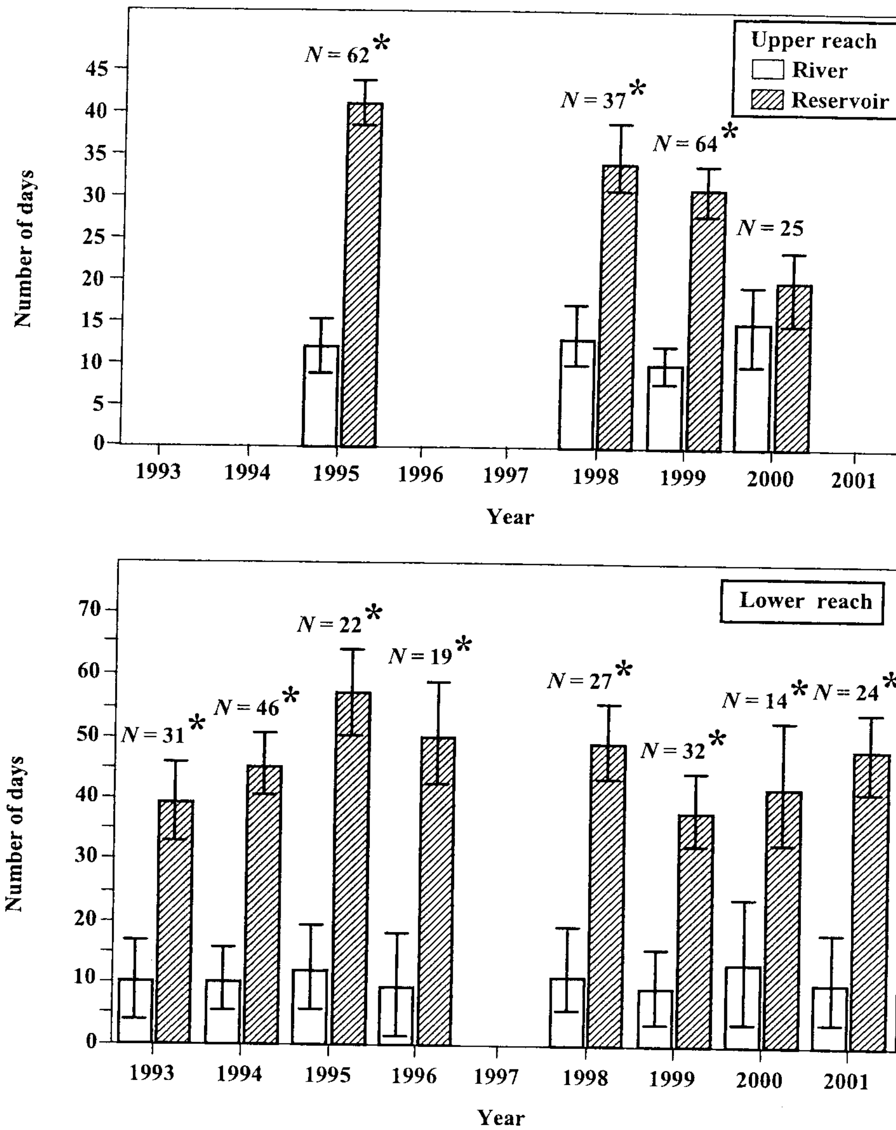

FIGURE 3.—Estimated annual least-squares mean number of days (with 95% confidence intervals) spent in the free-flowing Snake River and in Lower Granite Reservoir by PIT-tagged juvenile fall chinook salmon after initial tagging in the upper (top panel) and lower (bottom panel) reaches of the Snake River. Asterisks indicate a significant ($P < 0.05$) within-year difference in a pairwise comparison.

reservoir during all years except 2000 ($P = 0.0942$) (Figure 3).

A total of 215 PIT-tagged fall chinook salmon from the lower reach of the Snake River were both recaptured by beach seine and detected passing Lower Granite Dam during 1993–1996 and 1998–2001. The estimated annual mean number of days these fish spent in the free-flowing Snake River after initial tagging ranged from 9 to 13 d, and the annual mean number of days spent in Lower Granite Reservoir ranged from 38 to 57 d (Figure 3). Two-way ANOVA showed that the interaction between location and year was not significant ($F = 1.73$, $P < 0.1027$). The main effects of location and year were significant (location, $F = 472.47$, $P < 0.0001$; year, $F = 2.34$, $P = 0.0255$). After initial tagging, fish from the lower reach spent significantly ($P < 0.05$) fewer days in the river than in the reservoir during all years analyzed (Figure 3).

TABLE 2.—Least-squares mean rate of seaward movement (km/d; N and range in parentheses) by period and reach for fall chinook salmon that were PIT-tagged and released in the upper or lower reaches of the snake River, 1992–2001. Period 1 was the period from initial tagging in the Snake River to detection at Lower Granite Dam. Period 2 was the period from detection at Lower Granite Dam to detection at Little Goose Dam.

Year	Period 1		Period 2	
	Upper reach	Lower reach	Upper reach	Lower reach
1992		4.4 (39; 1.1–18.8)		
1993		2.1 (234; 0.7–19.7)		
1994		1.7 (193; 0.4–13.8)		
1995	4.6 (203; 1.1–44.8)	1.8 (237; 0.4–20.3)		
1996	6.2 (19; 2.1–43.8)	2.1 (125; 0.4–19.3)	20.0 (5; 15.0–30.0)	12.7 (39; 1.4–30.0)
1997	5.3 (22; 1.7–10.8)	3.3 (96; 0.6–21.6)	12.6 (9; 4.3–30.0)	7.5 (40; 0.8–30.0)
1998	4.4 (173; 1.6–20.1)	2.5 (380; 0.4–28.3)	17.4 (101; 1.2–30.0)	17.9 (188; 2.4–60.0)
1999	6.6 (319; 1.5–35.0)	3.0 (241; 0.7–19.5)	11.7 (113; 1.3–60.0)	13.4 (74; 1.5–60.0)
2000	6.6 (72; 2.6–19.9)	2.3 (257; 0.4–13.6)	12.1 (32; 1.6–30.0)	10.3 (121; 0.9–30.0)
2001	3.1 (13; 1.3–4.5)	2.1 (185; 0.5–15.0)	10.5 (6; 2.7–20.0)	8.1 (85; 0.6–30.0)

Rate of Seaward Movement by Reach

Totals of 821 PIT-tagged fall chinook salmon from the upper reach of the Snake River and 1,521 from the lower reach were detected passing Lower Granite Dam during1995–2001. The mean rate of seaward movement during period 1 (years 1995–2001) ranged from 3.1 to 6.6 km/d for fish from the upper reach, and from 1.8 to 3.3 km/d for fish from the lower reach (Table 2; Figure 4). Two-way ANOVA showed that the interaction between reach and year was significant (F = 7.46, P < 0.0001) but orderly, indicating the tests for main effects were appropriate. The main effects of reach and year on the $\log_e$ transformed rate of seaward movement were significant (reach, F = 391.82, P < 0.0001; year, F = 23.57, P < 0.0001). The $\log_e$-transformed rate of seaward movement was significantly (P < 0.05) and consistently higher for fish from the upper reach during period 1 (Figure 4).

The total number of PIT-tagged fall chinook salmon detected passing both Lower Granite and Little Goose dams during 1996–2001 was 266 for the upper reach of the Snake River and 547 for the lower reach. The mean rate of seaward movement during period 2 ranged from 10.5 to 20.0 km/d for fish from the upper reach, and from 7.5 to 17.9 km/d for fish from the lower reach (Table 2). The interaction between reach and year was not significant (F = 2.08, P < 0.0653) according to two-way ANOVA. The main effects of reach and year on the $\log_e$ transformed rate of seaward movement were significant (reach, F = 15.76, P < 0.0001; year, F = 9.74, P = 0.0019). The $\log_e$ transformed rate of seaward movement during period 2 was significantly (P = 0.0133) higher for fish from the upper reach in 1997, but not during 1996 and 1998–2001 (Figure 4).

Rate of Seaward Movement by Period

When testing for differences in the rate of seaward movement between periods 1 and 2 for fall chinook salmon PIT-tagged in the upper reach of the Snake River, the two-way ANOVA showed that the interaction between period and year was significant (F = 7.85, P < 0.0001). The interaction was orderly, therefore the tests for main effects were appropriate. The main effects of period and year were significant (period, F = 50.12, P < 0.0001; year, F = 2.67, P = 0.0227). The rate of seaward movement of fish from the upper reach was significantly (P < 0.05) higher during period 2 than during period 1, except in 2001 (P = 0.0961) (Figure 5).

Two-way ANOVA showed that the interaction between period and year was significant (F = 19.06; P < 0.0001) when testing for differences in the rate of seaward movement between periods 1 and 2 for fall chinook salmon PIT-tagged in the lower reach of the Snake River. Tests for main effects were appropriate because the interaction was orderly. The main effects of period and year were significant (period, F = 369.59, P < 0.0001; year, F = 19.47, P = 0.0227). The rate of seaward movement of fish from the lower reach was significantly ($P \leq 0.05$) and consistently higher during period 2 than during period 1 (Figure 5).

There was little evidence for a strong relation between the rate of seaward movement during period 1 and the probability of a PIT-tagged fall chinook salmon surviving and being detected at Little Goose Dam. Accuracy averaged 43.1%

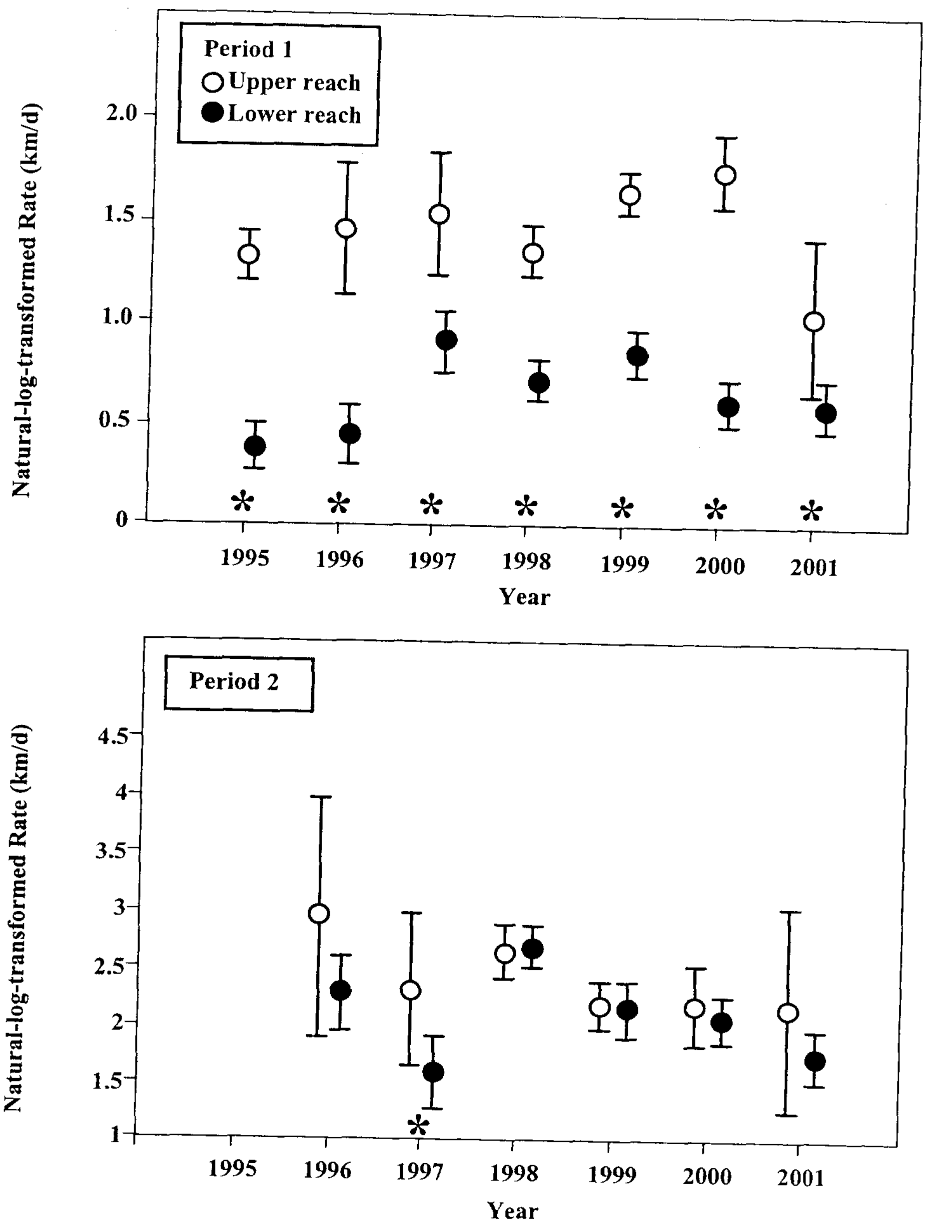

FIGURE 4.—Comparison of annual least-squares mean rates of seaward movement between PIT-tagged fall chinook salmon from the upper and lower reaches of the Snake River. Period 1 (top panel) was from initial tagging to detection at Lower Granite Dam, and period 2 (bottom panel) was from detection at Lower Granite Dam to detection at Little Goose Dam. Whiskers indicate 95% confidence intervals; asterisks indicate a significant ($P < 0.05$) within-year difference in a pairwise comparison.

(range, 22.7–73.7%) for the upper reach logistic regression models fitted from 1996–2001 data. The upper reach model predicted with 73.7% accuracy that every fish would survive to be detected at Little Goose Dam in 1996, and accuracy was high because more fish were detected (N = 14) than not detected (N = 5). For the lower reach logistic regression models fitted from 1996–2001 data, accuracy averaged 40.1% (range, 31.2–48.6%).

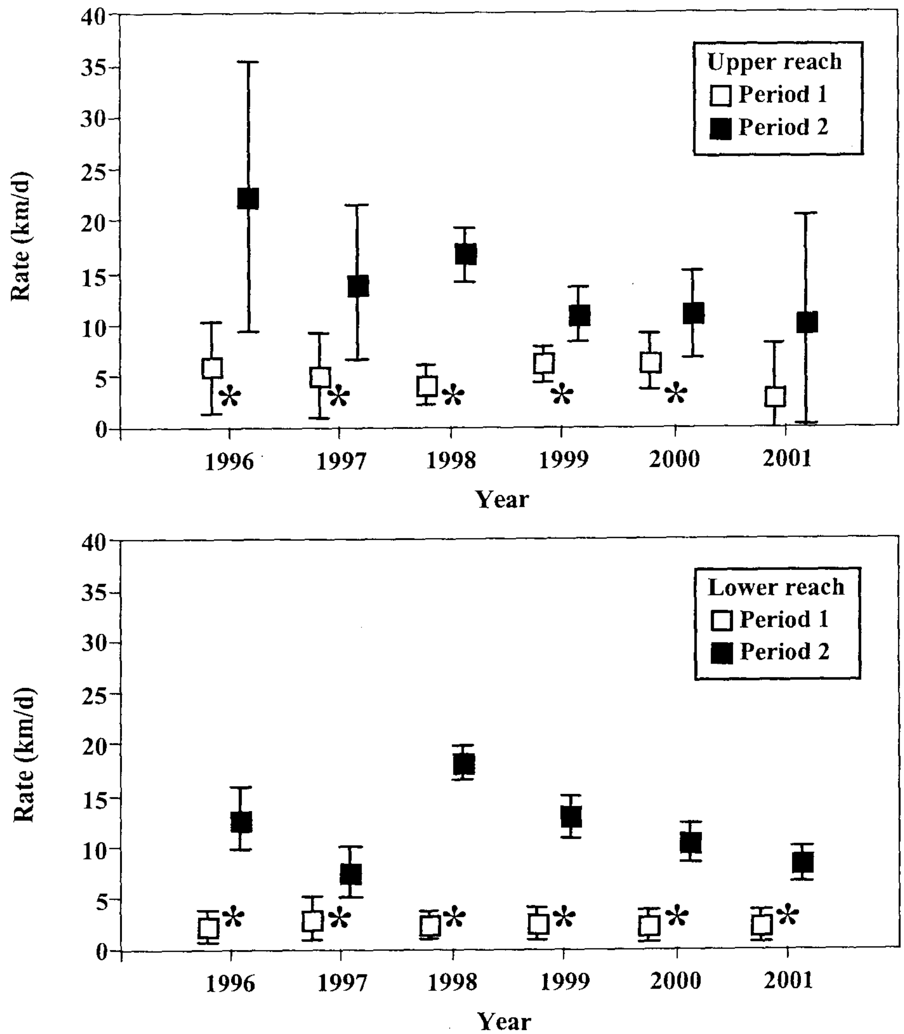

FIGURE 5.—Comparison of annual least-squares mean rates of seaward movement between periods for PIT-tagged fall chinook salmon from the upper (top panel) and lower (bottom panel) reaches of the Snake River. See Figure 4 for additional details.

Factors Affecting Rate of Seaward Movement during Period 1

A total of 2,808 observations were available (years 1992–2001) to describe the factors affecting the rate of seaward movement of PIT-tagged fall chinook salmon from initial tagging to detection at Lower Granite Dam (i.e., period 1; Tables 2, 3). The 1995–2001 data were used in the following year-by-year comparisons of the factors because fish were tagged in both reaches. Fish from the upper reach were exposed to higher flows and cooler temperatures in Lower Granite Reservoir than fish from the lower reach (Table 3). Fish were tagged earlier in the upper reach at slightly smaller fork lengths than fish in the lower reach (Table 3). Riverine distance traveled was longer for fish from the upper reach than for fish from the lower reach (Table 3).

After pooling the data across reaches and running every possible regression model, we found that the slope coefficient for flow changed from positive to negative when flow and temperature were entered into the same regression models. The correlation coefficient r for the relation between flow and temperature was -0.77 ($P < 0.0001$). The slope coefficient for tagging date changed from negative to positive when tagging date and temperature were entered into the same regression

TABLE 3.—Annual median values (ranges in parentheses) of the factors studied to describe the rate of seaward movement of PIT-tagged fall chinook salmon from initial tagging in the upper or lower reach of the Snake River to detection at Lower Granite Dam (i.e., period 1), 1992–2001. The factors include mean flow (m^3/s) in Lower Granite Reservoir between initial tagging and detection at Lower Granite Dam; mean temperature (°C) in Lower Granite Reservoir between initial tagging and detection at Lower Granite Dam; date of initial tagging (day of year); fork length (FL; mm) at initial tagging; and riverine distance traveled (km) to Lower Granite Dam.

Year	*N*	Flow	Temperature	Date	FL	Distance
			Upper reach			
1995	203	2,779 (1,452–3,880)	16.2 (13.2–19.2)	152 (131–173)	74 (60–108)	122 (95–137)
1996	19	3,826 (3,124–5,150)	13.1 (9.2–15.0)	137 (109–158)	69 (60–85)	124 (99–133)
1997	22	4,740 (3,332–5,158)	13.6 (11.6–16.2)	142 (128–157)	77 (62–104)	99 (90–133)
1998	173	3,434 (2,135–4,817)	15.1 (11.5–18.9)	140 (106–176)	73 (60–107)	99 (90–133)
1999	319	3,673 (1,604–4,872)	13.8 (11.3–18.6)	153 (126–183)	73 (60–112)	99 (90–141)
2000	72	1,982 (1,538–2,696)	15.1 (10.8–17.2)	146 (111–167)	80 (60–115)	128 (99–133)
2001	13	1,108 (633–1,478)	17.5 (14.3–20.1)	144 (116–158)	66 (60–81)	128 (124–142)
			Lower reach			
1992	39	1,075 (782–2,144)	16.5 (12.6–18.0)	147 (114–156)	76 (60–103)	27 (5–58)
1993	234	2,027 (1,005–4,243)	16.7 (12.2–19.6)	159 (117–195)	74 (60–122)	10 (0–42)
1994	193	1,029 (629–2,121)	18.9 (12.4–20.8)	152 (96–173)	76 (60–104)	26 (1–58)
1995	237	2,278 (1,187–3,541)	17.9 (14.0–20.4)	158 (116–187)	75 (60–114)	23 (2–66)
1996	125	2,740 (1,070–4,760)	15.8 (10.0–19.9)	156 (107–185)	73 (60–111)	7 (3–67)
1997	96	3,094 (1,354–5,127)	16.9 (12.8–20.2)	164 (140–191)	81 (60–108)	26 (1–63)
1998	380	2,783 (1,265–5,609)	16.5 (11.7–21.0)	154 (118–181)	76 (60–114)	30 (1–67)
1999	241	2,390 (1,397–4,568)	17.0 (11.2–20.1)	167 (118–189)	77 (60–111)	42 (3–67)
2000	257	1,775 (825–2,326)	16.1 (11.7–19.6)	152 (123–172)	75 (60–125)	27 (3–67)
2001	185	1,166 (750–1,836)	16.4 (12.3–20.0)	142 (115–171)	68 (60–115)	27 (17–67)

models. The correlation coefficient for the relation between tagging date and temperature was 0.60 ($P < 0.0001$). All models containing both flow and temperature, or tagging date and temperature, were removed from the analysis because of problematic multicollinearity.

The period 1 regression model with the best fit included the factors of temperature, fork length, and riverine distance (Table 4). The slope coefficients for each of the three factors differed significantly from zero, and together the three factors explained 73% of the variability observed in the $\log_e$ transformed rate of seaward movement (Table 4). The $\log_e$ transformed rate of seaward movement generally decreased as temperature increased, and increased as fork length and riverine distance increased, as shown by the sign and P-values of the slope coefficients (Table 4). The slope in the resid-

TABLE 4.—Results from ordinary-least-squares multiple regression models fitted to describe the factors affecting the rate of seaward movement of PIT-tagged fall chinook salmon from initial tagging in the Snake River (data pooled across reaches) to detection at Lower Granite Dam (i.e., period 1), 1992–2001. The factors include mean flow (m^3/s) in Lower Granite Reservoir between initial tagging and detection at Lower Granite Dam; mean temperature (°C) in Lower Granite Reservoir between initial tagging and detection at Lower Granite Dam; date of initial tagging (day of year); fork length (FL; mm) at initial tagging; and riverine distance traveled (km) to Lower Granite Dam.

Factor	Regression coefficient (b)	SE	t-value ($b = 0$)	Probability ($b = 0$)	R^2	P
Constant	0.81598	0.07490	10.89	<0.0001	0.726	<0.0001
Temperature	−0.15190	0.00382	−39.73	<0.0001		
FL	0.02773	0.00060	46.16	<0.0001		
Distance	0.00798	0.00018	44.42	<0.0001		
Constant	−2.07197	0.05627	−36.82	<0.0001	0.659	<0.0001
Flow	0.00024	0.00001	26.73	<0.0001		
FL	0.02496	0.00066	37.66	<0.0001		
Distance	0.00876	0.00020	43.88	<0.0001		
Constant	−1.17620	0.10755	−10.94	<0.0001	0.575	<0.0001
Date	−0.00304	0.00083	−3.68	0.0002		
FL	0.02568	0.00090	28.64	<0.0001		
Distance	0.01061	0.00022	49.56	<0.0001		

ual plot indicates that the rate of seaward movement decreased as temperature increased throughout the range of 9–21°C (Figure 6).

The period 1 regression model that had the second-best fit included the factors of flow, fork length, and riverine distance (Table 4). Flow, fork length, and riverine distance explained 66% of the variability observed in the $\log_e$ transformed rate of seaward movement. The $\log_e$ transformed rate of seaward movement generally increased with increases in each of the three factors based on the slope coefficients, all of which differed significantly from zero (Table 4). The slope in the residual plot shows that the rate of seaward movement increased as flow increased over the entire range of observed flows (Figure 6).

The period 1 regression model that had the third-best fit included the factors tagging date, fork length, and riverine distance (Table 4). The $\log_e$ transformed rate of seaward movement generally decreased with increases in tagging date, and increased as fork length and riverine distance increased, as shown by the signs and P-values of the slope coefficients (Table 4). Together, these three factors explained approximately 58% of the variability observed in the $\log_e$ transformed rate of seaward movement (Table 4).

Factors Affecting Rate of Seaward Movement during Period 2

A total of 813 observations were available (years 1996–2001) to describe the factors affecting the rate of seaward movement of PIT-tagged fall chinook salmon from detection at Lower Granite Dam to detection at Little Goose Dam (i.e., period 2; Tables 2, 5). Except in 2001, fish from the upper reach were exposed to slightly higher flows and cooler temperatures in Little Goose Reservoir than fish from the lower reach (Table 5). As shown previously, fish in the upper reach were slightly smaller at initial tagging than fish in the lower reach (Table 5). Fish from the upper reach were detected passing Lower Granite Dam earlier than fish from the lower reach (Table 5). Distance traveled from initial tagging to Little Goose Dam was longer for fish from the upper reach than for fish from the lower reach (Table 5). Fish from the upper reach had shorter travel times to Lower Granite Dam (i.e., the factor time; Table 5).

The correlation coefficients were relatively high between the factors of flow and temperature ($r = -0.73$, $P < 0.0001$), temperature and date ($r = -0.67$, $P < 0.0001$), fork length and travel time to Lower Granite Dam ($r = -0.63$, $P < 0.0001$), and detection date and travel time to Lower Granite Dam ($r = -0.66$, $P < 0.0001$). However, we found no evidence for problematic multicollinearity among the period 2 factors after pooling the data across reaches and years and running every possible regression model.

The period 2 regression model that had the best fit included the variables flow, temperature, fork length, detection date at Lower Granite Dam, and travel time to Little Goose Dam (Table 6). However, this model only explained 19% of the variability observed in the $\log_e$ transformed rate of seaward movement (Table 6). The slope coefficients of every factor in the regression model differed significantly ($P < 0.05$) from zero (Table 6), but the significance likely resulted from the large sample size of fish ($N = 813$).

Discussion

Migrational Phases

Beach seine catch declined after May, when fork length averaged 56–61 mm. Fork length averaged 86–92 mm at the end of the seining season, when the large majority of fall chinook salmon had moved into Lower Granite Reservoir. These results suggest that offshore movement and downstream dispersal typically began in late spring as fish approached 60 mm FL, and that most fall chinook salmon moved offshore and into Lower Granite Reservoir before growing to 90 mm FL. Initiation of offshore movement by juvenile anadromous salmonids associated with growth in fork length has been observed by others (Chapman and Bjornn 1969; Lister and Genoe 1970; Everest and Chapman 1972). In the free-flowing Columbia River, subyearling chinook salmon captured in fyke nets positioned offshore were longer than those captured along the shoreline (Dauble et al. 1989).

The histories of PIT-tagged fall chinook salmon that were recaptured after initial tagging provide insight into migrational behavior of fish inhabiting shoreline waters. The majority of fish that were recaptured had not moved from initial tagging locations, suggesting periods of residency. The small number of fish recaptured downstream of initial tagging locations indicates either that some fish remained nearshore when dispersing downstream or that some fish regained shoreline contact after periods of downstream dispersal offshore. The recaptured fish that moved downstream from the upper reach of the Snake River traveled farther at higher rates than their counterparts from the lower reach. The longer dispersal distances and higher

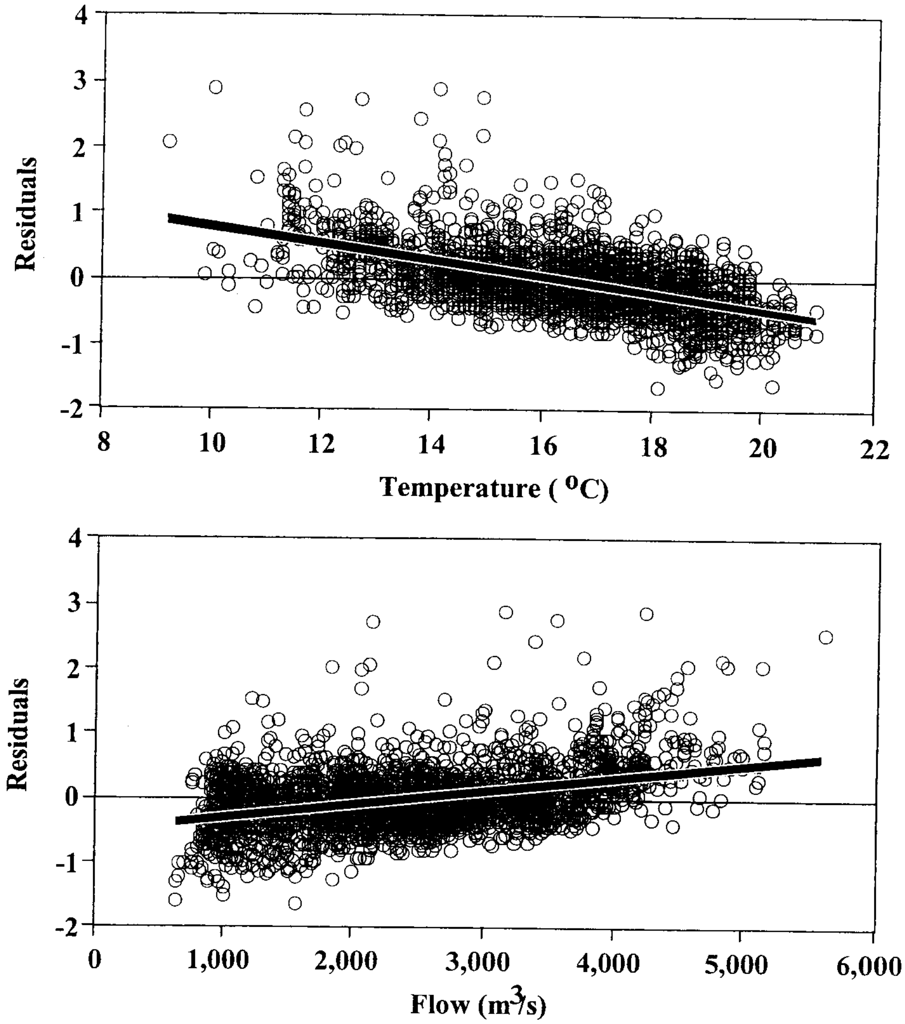

FIGURE 6.—Residual plots for temperature (top panel) and flow (bottom panel). Residuals are from ordinary-least-squares multiple regression models fitted from fork length (mm) at initial tagging and riverine distance traveled (km) to Lower Granite Dam. The line in each plot was predicted by regressing the residuals against the factor on the *x*-axis.

dispersal rates of fish from the upper reach were likely tied to habitat connectivity and channel gradient.

Large majorities (85% and 89%) of the fall chinook salmon that we PIT-tagged in the upper and lower reaches of the Snake River were never recaptured during beach seining. In terms of migrational behavior, the best explanation for this result is abrupt downstream dispersal into Lower Granite Reservoir resulting from loss of contact with the rearing area and exposure to relatively high offshore water velocities (e.g., Hoar 1958). Use of weekly versus continuous sampling, less than 100% capture efficiency, and fish mortality were also likely factors contributing to the low rate of recapture.

Assuming that fish moved rapidly into the reservoir after last being recaptured, we estimated that passage in Lower Granite Reservoir occupied the majority of days that elapsed between the initial tagging and detection of PIT-tagged fall chinook salmon at Lower Granite Dam. A comparison of results from other studies (Curet 1994; Connor et al. 2002; D. H. Bennett, University of Idaho, unpublished data) suggests that juvenile fall chinook salmon remained offshore after entering

TABLE 5.—Annual median values (ranges in parentheses) of the factors studied to describe the rate of seaward movement of PIT-tagged fall chinook salmon (data pooled across reaches) from detection at Lower Granite Dam to detection at Little Goose Dam (i.e., period 2), 1996–2001. Data are presented by reach. The factors include mean flow (m^3/s) in Little Goose Reservoir between detection at Lower Granite and Little Goose dams; mean temperature (°C) in Little Goose Reservoir between detection at Lower Granite and Little Goose dams; detection date (day of year) at Lower Granite Dam; fork length (FL; mm) at initial tagging in the Snake River; total distance traveled (km) from initial tagging to Little Goose Dam; and travel time (d) between initial tagging and detection at Lower Granite Gam.

Year	*N*	Flow (m^3/s)	Temperature (°C)	Date	FL (mm)	Distance (km)	Time (d)
				Upper reach			
1996	5	1,520 (1,282–2,202)	21.2 (18.0–21.6)	192 (186–201)	76 (64–85)	235 (210–244)	50 (35–65)
1997	9	2,182 (1,382–3,828)	17.6 (15.5–20.2)	185 (168–225)	76 (68–89)	210 (201–244)	48 (13–90)
1998	101	1,837 (1,452–5,107)	20.2 (11.9–22.6)	188 (145–209)	73 (60–107)	216 (201–244)	44 (7–69)
1999	113	2,037 (1,021–4,260)	17.2 (11.8–23.0)	179 (158–224)	74 (60–112)	210 (201–248)	31 (6–83)
2000	32	1,167 (991–2,171)	18.7 (13.2–20.1)	178 (127–187)	82 (61–115)	239 (210–244)	31 (9–63)
2001	6	748 (729–762)	21.3 (20.3–23.4)	196 (185–223)	67 (62–81)	239 (235–253)	50 (40–94)
				Lower reach			
1996	39	1,373 (811–2,645)	21.3 (14.6–23.4)	197 (164–236)	69 (60–111)	118 (114–178)	48 (15–94)
1997	40	1,720 (888–2,983)	18.9 (16.5–20.9)	193 (172–265)	82 (60–108)	119 (112–174)	30 (5–95)
1998	188	1,799 (600–2,731)	20.4 (15.8–22.9)	190 (168–240)	78 (60–114)	141 (112–178)	38 (10–73)
1999	74	1,399 (966–4,064)	20.0 (13.3–23.0)	202 (160–231)	77 (60–110)	151 (118–174)	39 (5–75)
2000	121	1,111 (556–1,875)	19.2 (15.3–21.0)	184 (139–253)	73 (60–116)	145 (114–178)	40 (8–100)
2001	85	761 (415–1,019)	21.0 (15.6–23.7)	186 (155–267)	68 (60–107)	138 (128–178)	50 (15–118)

Lower Granite Reservoir. For example, in 1992, beach seine catch at stations in both the free-flowing Snake River and Lower Granite Reservoir declined concurrently to zero (Curet 1994; Connor et al. 2002). This would not be expected if fish from the free-flowing river moved downstream gradually along the shoreline when entering the reservoir.

The rate of seaward movement increased markedly between periods 1 and 2 for fall chinook salmon from both reaches of the Snake River. We found no evidence that this increase was caused by the

TABLE 6.—The best ordinary-least-squares multiple model fitted to predict the rate of seaward movement of PIT-tagged fall chinook salmon from detection at Lower Granite Dam to detection at Little Goose Dam (i.e., period 2), 1996–2001. The factors include mean flow (m^3/s) in Little Goose Reservoir between detections at Lower Granite and Little Goose dams; mean temperature (°C) in Little Goose Reservoir between detections at Lower Granite and Little Goose dams; detection date (day of year) at Lower Granite Dam; fork length (FL; mm) at initial tagging in the Snake River; and travel time (d) between initial tagging and detection at Little Goose Dam.

Factor	Regression coefficient (*b*)	SE	*t*-value (*b* = 0)	Probability (*b* = 0)	R^2	*P*
Constant	−3.18995	0.51327	−6.21	<0.0001	0.185	<0.0001
Flow (m^3/s)	0.00066	0.00006	12.03	<0.0001		
Temperature (°C)	0.18938	0.02045	9.26	<0.0001		
Date	−0.00738	0.00281	−2.63	0.0088		
FL (mm)	0.01901	0.00326	5.84	<0.0001		
Time (d)	0.01708	0.00314	5.44	<0.0001		

survival of inherently fast migrants. Thus, the change in the rate of seaward movement reflects a change in migrational behavior. Fall chinook salmon from both the upper and lower reaches grow rapidly (1.0–1.4 mm/d) to fork lengths associated with successful smoltification (mean ± SD, 141 ± 15 mm) by the time they are detected at Lower Granite Dam (Connor and Burge 2003). We did not study physiological development; however, we suspect that fish became progressively more migratory as they passed downstream because they were becoming smolts (e.g., Zaugg et al. 1985).

We conclude that young fall chinook salmon passed through at least four migrational phases as they moved seaward and that these phases can be characterized by the habitat fish occupied and changes in the rate of seaward movement. The four phases are (1) discontinuous downstream dispersal along the shorelines of the free-flowing river; (2) abrupt and mostly continuous downstream dispersal offshore in the free-flowing river; (3) passive, discontinuous downstream dispersal offshore in Lower Granite Reservoir; and (4) active and mostly continuous seaward migration in Lower Granite Reservoir as fish become smolts.

Factors Affecting Rate of Seaward Movement during Period 1

Discussing the results of our analyses on the rate of seaward movement of PIT-tagged fall chinook salmon from initial tagging to detection at Lower Granite Dam (i.e., period 1) requires an understanding of the limitations on our study. We could not calculate rates of seaward movement for fish that were not detected at Lower Granite Dam. If there were nonrandom differences between the population that was detected at Lower Granite Dam and the population that was not detected at Lower Granite Dam, the true relation between the rate of seaward movement and the factors we studied might be different from the regression results we reported. Another limitation on our study was that the rates of seaward movement reported for period 1 were slightly inaccurate because fall chinook salmon rarely pass dams on initial approach (Venditti et al. 2000). For example, radio-tagged fall chinook salmon took an average of about 1 d to pass Little Goose Dam after initially encountering the dam (Venditti et al. 2000). Therefore, the period 1 rates of seaward movement were slightly lower than the true rates to Lower Granite Dam forebay because travel times to Lower Granite Dam (years 1992–2001; median, 43 d; range, 3–170 d) used to calculate the rate of seaward movement were about 1 d too long. Calculating mean flows and temperatures from data collected at Lower Granite Dam also influenced the fit of period 1 regression models because these means were only surrogates for the local velocities and temperatures where the fish actually migrated.

The period 1 regression model that predicted the $\log_e$ transformed rate of seaward movement from the factors of temperature, fork length, and riverine distance had the best fit of all models tested. It is unrealistic, however, to expect an inverse relation between temperature and rate of seaward movement over the entire range of temperatures studied (9–21°C). Fall chinook salmon that are exposed to mean temperatures of 20°C and above before they become smolts would be expected to move seaward at slower rates than those that experience cooler temperatures because of a reduced likelihood of successful smoltification (e.g., Marine 1997). However, the rate of seaward movement should have increased as temperature increased up to at least 17°C as a result of increased growth and normal patterns of smolt development (Banks et al. 1971; Boeuf 1993; Marine et al. 1997; Beckman et al. 1998; Connor and Burge 2003). The decrease in the rate of seaward movement as temperature increased to 17°C was most likely caused by the accompanying decreases in flow during summer.

The period 1 regression model with the second-best fit included the factors of flow, fork length, and riverine distance. This regression model showed that the relation between the rate of seaward movement and flow was positive, consistent with the results of other studies (Berggren and Filardo 1993; Tiffan et al. 2000). Higher rates of seaward movement at higher flows (or vice versa) can be explained by the relation between discharge and water velocity. Water velocity in reservoirs is proportional to the ratio of discharge to channel volume. Because the length of Lower Granite Reservoir presumably changes little over time, the change in volume can be described by changes in pool elevation. Lower Granite Reservoir was held at minimum operating pool elevations ranging from approximately 223 to 224 m above mean sea level during the summer (U.S. Army Corps of Engineers, unpublished data). Therefore, the flow values we used in our regression modeling were proportional to velocities in Lower Granite Reservoir upstream of Lower Granite Dam forebay, suggesting that the rate of seaward movement increased as velocity increased.

The rate of seaward movement during period 1 decreased as tagging date increased, according to the results of the regression model with the third-best fit. Tagging date (release date) is used as a surrogate for time-based physiological, behavioral, and environmental processes when describing seaward movement of juvenile anadromous salmonids (e.g., Berggren and Filardo 1993; Giorgi et al. 1997; Connor et al. 2000). There was no significant tagging date effect when flow and tagging date were entered into the same regression model. Problems with multicollinearity were encountered when tagging date and temperature were entered into the same regression model. In our analyses, tagging date apparently functioned as a surrogate for flow and temperature and possibly the decreased potential for successful smoltification of fish initially tagged late in the seining season.

The rate of seaward movement was positively related to fork length in all three of the period 1 regression models. Previously discussed results support the hypothesis for fork length-related offshore movement, which would place larger fish in faster flowing water than smaller fish and facilitate downstream dispersal. Young anadromous salmonids are also thought to become smolts at a critical size, or while growing rapidly over a continuum of fork lengths (Folmar and Dickhoff 1980; Wedemeyer et al. 1980; Beckman and Dickhoff 1998; Beckman et al. 1998; Connor et al. 2001a).

The rate of seaward movement was positively related to riverine distance in all three of the period 1 regression models. There are two plausible explanations for this finding. First, fall chinook salmon that were PIT-tagged at upstream locations passed through longer stretches of free-flowing river with higher channel gradients (hence, higher velocities) than those experienced by fish tagged closer to the upper end of Lower Granite Reservoir. Secondly, level of smoltification and migrational disposition might have increased with distance traveled (Zaugg et al. 1985).

We conclude that the rate of seaward movement of fall chinook salmon during period 1 was influenced by flow, temperature, fork length, and riverine distance. There was little difference in fork length between PIT-tagged fish in the upper and lower reaches of the Snake River (upper-reach fish were slightly smaller). Fish from the upper reach of the Snake River may have moved seaward at higher rates than fish from the lower reach because they were exposed to higher flows and lower temperatures, and they traveled through a longer stretch of free-flowing river with a higher channel gradient and higher velocities.

Factors Affecting Rate of Seaward Movement during Period 2

Our analyses on the rate of seaward movement of PIT-tagged fall chinook salmon between detections at Lower Granite and Little Goose dams (i.e., period 2) were subject to the same limitations discussed for period 1. However, a forebay delay of 1 d (Venditti et al. 2000) would make up a much larger portion of the total travel time to Little Goose Dam (years 1996–2001; median, 5 d; range, 1–96 d) than to Lower Granite Dam. Therefore, forebay delay probably had a much larger effect on the rate of seaward movement during period 2 than during period 1.

Given the study limitations, the results in this paper fail to support a causal linkage between the factors studied and the rate of seaward movement of PIT-tagged fall chinook salmon during period 2. The rate of seaward movement during period 2 was largely similar between fish from the upper and lower reaches of the Snake River, even though fish from the upper reach were exposed to higher flows and cooler temperatures, passed Lower Granite Dam earlier, migrated longer distances to Little Goose Dam, and spent more time developing physiologically in-river. Furthermore, the best regression model for describing the rate of seaward movement of PIT-tagged fall chinook salmon during period 2 explained very little (19%) of the variability observed in the $\log_e$ transformed rate of seaward movement.

Management Implications

We conclude that the increases in flow and decreases in temperature resulting from summer flow augmentation increase the rate of seaward movement of fall chinook salmon in Lower Granite Reservoir (where fish spend prolonged periods of time), provided that augmentation occurs when the fish have moved offshore in the free-flowing river and are behaviorally disposed to being displaced downstream. The regression model that included flow predicts an increase in the rate of seaward movement of approximately 0.1 km/d with each increase of 100 m^3/s in flow, when fork length and riverine distance are held at 74 mm and 40 km (the overall 1992–2001 medians). At temperatures above 17°C, the regression model that included temperature predicts an increase in the rate of seaward movement of approximately 0.2 km/d with each decrease of 1°C, when fork length and riverine distance are held at 74 mm and 40 km. Increasing the rate of seaward movement by 0.1–0.2 km reduces travel time to Lower Granite Dam by 1–6 d (Connor 2001).

Flow and temperature effects on the rate of seaward movement of PIT-tagged fall chinook salmon in Little Goose Reservoir were not apparent in our study. However, temperature simulations for the upper end of Little Goose Reservoir during 1998–2000 indicate that summer flow augmentation prevented temperatures from reaching daily averages in the range of 22–24°C (Connor et al. 2003). Even if the rate of seaward movement is not linearly dependent on flow and temperature, warm temperatures in the absence of summer flow augmentation might disrupt growth and normal patterns of smoltification.

Information on the local velocities and temperatures where fall chinook salmon migrate, as well as on forebay delay and mortality, is necessary to more fully understand the effect of summer flow augmentation on the rate of seaward movement. Radio-tagging studies are needed to expand on the work of Venditti et al. (2000) in order to learn how fish respond to changes in local velocities as they pass downstream in riverine and reservoir habitats. Studies are also needed to expand on the work of Marine (1997), Mesa et al. (2002), and Connor and Burge (2003) so that temperature effects on fall chinook salmon physiology, growth, and migrational behavior can be more fully understood.

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