Late-season mortality during migration of radio-tagged adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River

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Abstract: We radio-tagged 577 adult sockeye salmon (*Oncorhynchus nerka*) returning to the Columbia River in 1997 to determine how migration behaviors were related to migration success in an altered river system. The probability of successful migration declined dramatically for late-entry individuals, concomitant with declines in discharge and the onset of stressful temperatures. Long dam passage times were not related to unsuccessful migration at most dams. However, when migration histories were analyzed across multiple dams or reservoirs, relatively slow migration was significantly associated with unsuccessful migration, suggesting potential cumulative effects. Median passage times at dams were rapid (7.9–33.4 h), although 0.2%–8% of salmon took more than 5 days to pass. Reservoir passage was also rapid, averaging 36.8–61.3 km·day^{-1}, and appeared to compensate for slowed migration at dams. Rates observed in the unimpounded Hanford Reach suggest that total predam migration rates may have been similar to current rates. Overall, our results suggest that cumulative effects may be more important than negative effects of passage at single dams and that hydrosystem alteration of temperature regimes in the migration corridor may have an important indirect negative impact on adults.

Résumé : Nous avons muni d'émetteurs radio 577 saumons rouges (*Oncorhynchus nerka*) qui retournaient dans le Columbia, afin de déterminer de quelle manière les comportements migrateurs sont reliés au succès de la migration dans un système hydrographique modifié. La probabilité d'une migration réussie diminue de façon spectaculaire chez les individus qui arrivent tard, au moment où le débit diminue et où les températures accablantes s'installent. Dans la plupart des barrages, la durée prolongée de traversée n'est pas reliée à l'insuccès de la migration. Cependant, lorsque le parcours de la migration au travers plusieurs barrages et réservoirs est analysé, il y a une relation significative entre une migration relativement lente et l'insuccès de la migration, ce qui indique la possibilité d'effets cumulatifs. La durée médiane du passage des barrages est courte (7,9–33,4 h), bien que 0,2–8 % des poissons mettent plus de 5 jours à les traverser. La traversée des réservoirs est aussi rapide, à une vitesse moyenne de 36,8–61,3 km·jour^{-1}, et semble compenser le ralentissement de la migration aux barrages. Les taux observés dans la section Hanford qui ne contient pas de réservoir indiquent que les taux de migration avant l'érection des barrages ont dû être semblables aux taux actuels. En gros, nos résultats indiquent que les effets cumulatifs peuvent être plus importants que les effets négatifs causés par le passage des barrages individuels et que la modification des régimes thermiques du système hydrographique dans le corridor de migration peut avoir un important impact négatif indirect sur les adultes.

[Traduit par la Rédaction]

Introduction

Returns of wild Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) in the Columbia River basin have declined dramatically from historic levels (Raymond 1988; McClure et al. 2003). Declines have been attributed primarily to development of the Columbia River for hydroelectric power, overharvest, habitat loss, and hatcheries (Raymond 1988; National Research Council 1996; Ruckelshaus et al. 2002). Currently, 12 Columbia basin salmon and steelhead evolutionarily significant units are listed as endangered or threatened under the US Endangered Species Act (National Marine Fisheries Service 2000), including one sockeye salmon (*Oncorhynchus nerka*) run. Hydroelectric dams have transformed the river into a series of reservoirs punctuated by dams extending through much of the migra-

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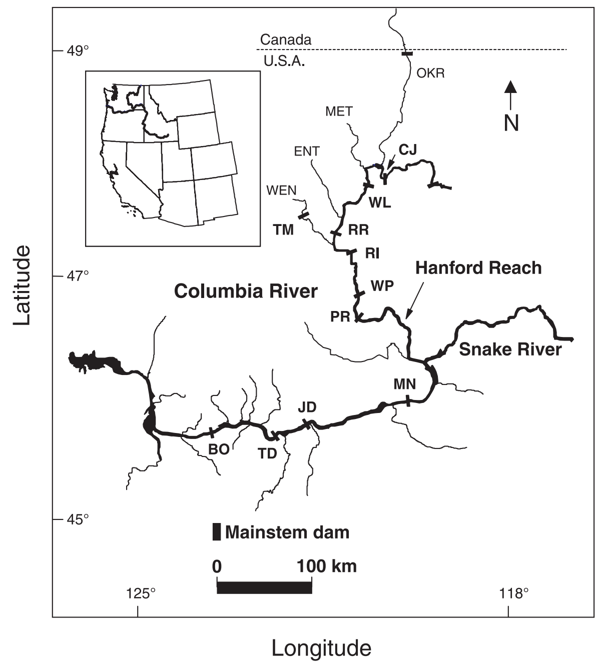
tion corridor. Despite this dramatic change, relatively little is known about the behavior and survival of adult salmon, particularly sockeye salmon, as they migrate upstream, and there is concern that dams may slow migration, subsequently reducing escapement to spawning grounds, population viability, and species recovery (Quinn et al. 1997; Dauble and Mueller 2000).

The construction of Grande Coulee Dam in 1939 blocked sockeye access to habitat in the upper Columbia River, and consequently, the majority of Columbia basin sockeye salmon stocks went extinct (Nehlsen et al. 1991). Adult sockeye salmon enter the Columbia River in early summer (Quinn et al. 1997) with peak counts at Bonneville Dam primarily in June and July and spawn in tributaries in September and October. Columbia River sockeye salmon stocks are primarily wild, native and are found in few drainages in the basin (Mullan 1986; Fryer 1995). Currently, most sockeye salmon spawn in tributaries to Lakes Wenatchee (Wenatchee River basin) and Osoyoos (Okanogan River basin) (Fig. 1) in September and October (Mullan 1986; Quinn et al. 1997). These lakes are 842 and 946 km from the mouth of the Columbia River, respectively, and comprise <4% of the historical sockeye salmon nursery habitat in the upper Columbia River basin (Gustafson et al. 1997). These stocks are not listed under the Endangered Species Act, although Nehlsen et al. (1991) classified the stocks as of special concern. The Snake River sockeye salmon evolutionarily significant unit is listed as endangered because of critically low population size, and thus, the Wenatchee River and Okanogan River evolutionarily significant units account for nearly all remaining sockeye salmon in the Columbia basin (Quinn and Adams 1996). The Wenatchee and Okanogan stocks pass seven and nine dams, respectively, to reach spawning tributaries.

In addition to representing a migration barrier, there is concern that dams and other forces including changes in land use and regional climate have altered the thermal regime encountered by migrating salmon. Temperatures >20 °C are physiologically stressful to salmonids (Becker and Fujihara 1978; McCullough et al. 2001), including sockeye salmon (Brett 1965; Gilhousen 1990), and temperatures above 24 °C are thought to be lethal to migrating adult salmon (Servizi and Jensen 1977). Warm summer temperatures are thought to constrain the run timing of salmon (e.g., Quinn and Adams 1996; Hodgson and Quinn 2002), and water temperatures in the mainstem Columbia River consistently exceed these values in summer. In particular, indirect data from historical dam counts support the hypothesis that earlier warming and higher summer temperatures over the last half century have led to earlier run timing in Columbia River sockeye salmon (Quinn and Adams 1996; Quinn et al. 1997). Many factors may contribute to the warming trend of the Columbia River including irrigation and land use practices (Coutant 1999), heating caused by greater residence time of water in impoundments (Quinn and Adams 1996), and perhaps regional climate change (Neitzel et al. 1991; Hamlet and Lettenmaier 1999).

We used our observational telemetry data to address several questions related to basic salmon biology and the management of salmon in an impounded system. We asked the following. Was migration success (defined as survival to a spawning tributary) related to behavior during dam passage and (or) environmental conditions encountered during migration? What was the seasonal pattern of migration success? What were the general daily and seasonal patterns of migration and how were environmental factors related to dam passage and reservoir migration behavior? How did migration behavior at dams and in reservoirs compare? We also discuss how migration success and straying compared with sockeye migration in other river systems and with migration by other Columbia River salmon species. Finally, we use migration data from a single 70-km unimpounded reach to speculate about whether current migration rates through the hydrosystem differed from the historic condition.

Fig. 1. Map of the study region in the northwestern United States (inset) including the location of radio receivers at dams and major tributaries within the Columbia River study area in 1997. Receiver locations at mid-Columbia River and tributary sites are maintained by the Chelan and Douglas County public utility districts. Dam abbreviations: BO, Bonneville; TD, The Dalles; JD, John Day; MN, McNary; PR, Priest Rapids; WP, Wanapum; RI, Rock Island; RR, Rocky Reach; WL, Wells; TM, Tumwater; CJ, Chief Joseph. Tributary abbreviations: WEN, Wenatchee River; ENT, Entiat River; MET, Methow River; OKR, Okanagan River.

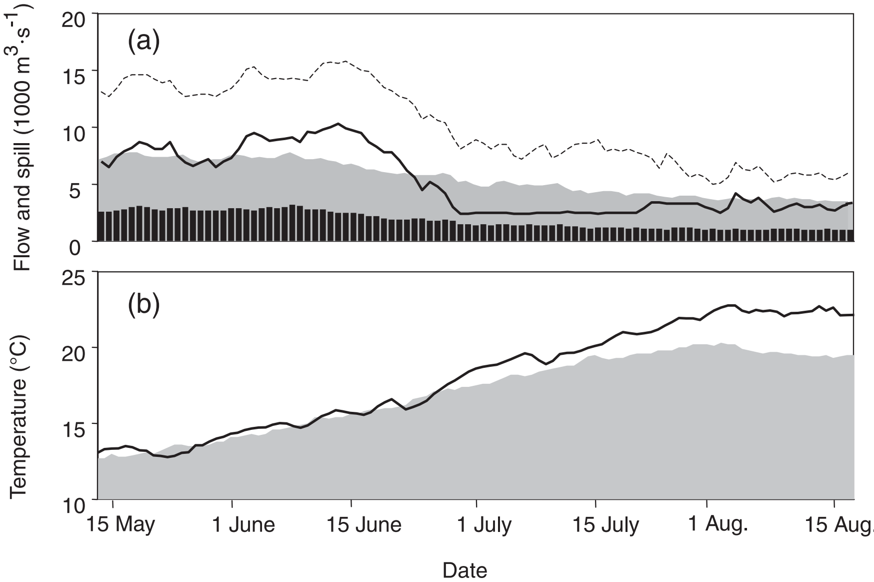


Methods

Study system

The Columbia River study area included four mainstem dams and reservoirs in the lower Columbia River (Bonneville, The Dalles, John Day, and McNary) and five mid-Columbia River dams and reservoirs (Priest Rapids, Wanapum, Rock Island, Rocky Reach, and Wells) and all major tributaries between Bonneville and Chief Joseph dams on the Columbia River (Fig. 1). The University of Idaho Cooperative Fish and Wildlife Research Unit maintained radio receivers and antennas at dams and tributaries between Bonneville and Wanapum dams, while concurrent telemetry projects by the

Fig. 2. Plots of (*a*) mean river discharge and discharge over the spillway and (*b*) temperature conditions at Bonneville Dam from 1987 to 1996 and during 1997. Fig. 2*a*: the broken line represents flow, the solid line represents spill, shading represents 1987–1996 flow, and bars represent 1987–1996 spill. Fig. 2*b*: the line represents 1997 temperature and shading represents 1987–1996 temperature. The seasonal patterns of flow, spill, and temperature conditions at the other Columbia River dams were similar. Both discharge and spill during the study period were unusually high at all dams.



Chelan and Douglas County public utility districts (Alexander et al. 1998) provided data from Rock Island, Rocky Reach, Wells, and Chief Joseph dams. The University of Idaho Cooperative Fish and Wildlife Research Unit also monitored mainstem and tributary sites with mobile radio-tracking units, and additional data were collected from hatcheries, fisheries and spawning ground surveys. All Columbia River stocks of sockeye salmon tagged at Bonneville Dam could therefore be tracked to spawning tributaries.

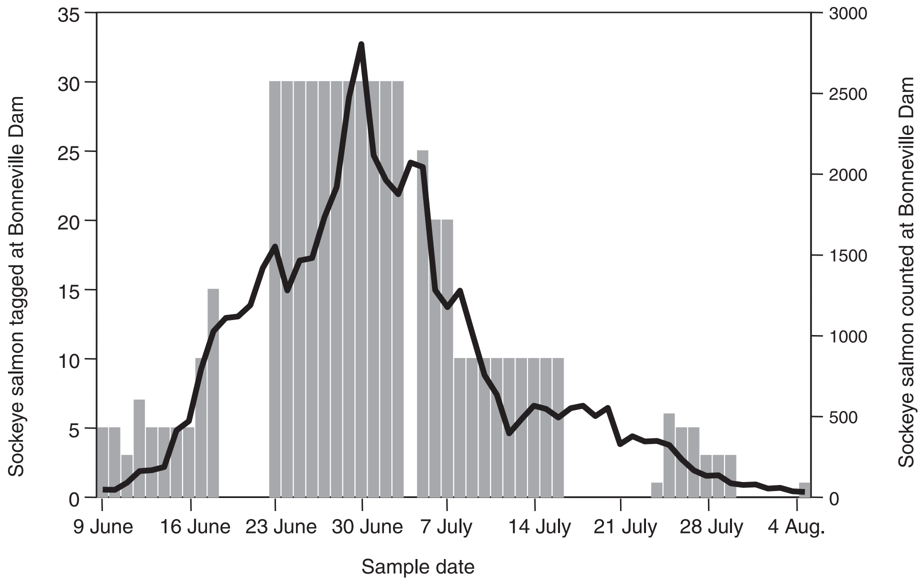
River conditions during the 1997 study were characterized by high flows. Mean daily Columbia River discharge in June and July was 10 724 $m^3 \cdot s^{-1}$, nearly double the 10-year average (1987–1996) of 5635 $m^3 \cdot s^{-1}$. Consequently, discharge over the spillway of dams (spill) during the sockeye salmon migration was often several times higher than average (Fig. 2). Water temperatures in the lower Columbia River ranged from about 13 °C in early June to 23 °C in late August, levels that were near average (Fig. 2). Mean summer water temperatures in the mid-Columbia River upstream from the Snake River confluence averaged 3–5 °C cooler than in the lower Columbia River. Despite the high discharge conditions, water temperatures were warmer than average after June (Fig. 2).

Trapping and tagging

Adult sockeye salmon were trapped for intragastric radio-tagging (Mellas and Haynes 1985) in the adult fish facility adjacent to the Washington-shore ladder at Bonneville Dam as they migrated upstream using the techniques described in greater detail by Keefer et al. (2004*a*). The fish were radio-tagged using 3-V radio transmitters (Lotek Wireless, Inc., Newmarket, Ontario) that transmitted a unique digitally coded signal every 5 s. Radio-tags were cylindrical and weighed 11 g in air (4.3 cm × 1.4 cm). After tagging, fish were moved to a 2275-L oxygenated, insulated transport tank and were then released within 6.2 h (mean = 1.96 h, SD = 1.05 h, range = 0.43–6.20 h) at locations 9.5 km downstream from Bonneville Dam on both sides of the river. No sockeye salmon mortalities occurred during tagging, transport, or release.

We radio-tagged 577 sockeye salmon between 9 June and 5 August approximately in proportion to daily run counts (Fig. 3). The tagged fish represented 1.2% of the 46 665 sockeye salmon counted passing Bonneville Dam during the tagging period. We tagged all fish regardless of minor injury or fin clip. Fish with severe injuries (e.g., gashes penetrating to the coelomic cavity or those that affected swimming performance) accounted for <1% of all fish trapped and were not tagged. The exclusion of these fish may have led to a slight (<1%) overestimation of survival, but we do not expect that this bias would affect our estimates of migration behavior. While we selected fish haphazardly and tagged them in approximate proportion to the number passing the dam each day, the samples were not truly random because only fish passing through one of the two Bonneville ladders were sampled. Further, the proportion sampled each day varied slightly, and we did not sample at night because few sockeye salmon pass dams at night (Quinn and Adams 1996; Results). We estimated that 72% of the 577 radio-tagged fish were male and 28% were female, a sex ratio typical in returning sockeye (e.g., Gustafson et al. 1997). Sixty-nine percent of the fish that entered tributaries were males (n = 267) compared with 31% female (n = 121), proportions similar to those at the time of tagging (χ^2 test, p = 0.24, n = 574). Five fish (0.9%) had adipose or ventral fin clips, and 99.1% were unclipped, presumably wild fish. Fork lengths of tagged fish ranged from 38 to 63 cm (median = 49.5 cm) and mean fork lengths of radio-tagged sockeye salmon that entered

Fig. 3. Number of sockeye salmon outfitted with radio transmitters at the Bonneville Dam adult fish facility (bars) and the number counted passing the dam at the counting stations (line) during the migration in 1997.



Wenatchee tributaries (including White River fish, mean = 50.3 cm, range 38–61 cm) were slightly larger than those entering the Okanogan River (mean = 48.8 cm, range 43–56 cm; separate variances *t* test, $t = -5.074$, $p < 0.001$, $n = 384$).

Telemetry monitoring and fate assignment

Fixed radiotelemetry sites were the primary means of assessing movements and passage rates of radio-tagged sockeye salmon. We used SRX receivers (Lotek Wireless, Inc.) with aerial Yagi antennas to monitor tailrace areas at dams and tributary mouths and digital spectrum processors added to SRX receivers with underwater antennas made of coaxial cable to monitor fishways and ladder exits at dams. On average, receivers operated >90% of the time at lower Columbia River dams and >80% of the time at Priest Rapids and Wanapum dams (Table 1). Trucks and boats outfitted with aerial antennas were used to track fish in areas not covered by fixed-site receivers, including mainstem reservoirs, accessible tributaries, and the Hanford Reach below Priest Rapids Dam. At the Wenatchee River, fixed site receivers were deployed at the mouth and at Tumwater Dam (53 km upstream from the mouth). Mobile tracking upstream from Wells Dam was conducted approximately every 2 weeks from late July to early November, a period much shorter than the typical period between arrival in the Okanogan River and the initiation of spawning (Hodgson and Quinn 2002).

We used a combination of telemetry records, spawning ground surveys, and radio-tag returns from fisheries to classify fish as successful migrants or as mortalities. Successful migrants included salmon with telemetry records in known spawning tributaries, those found as carcasses in spawning tributary surveys, or those that returned to their hatchery of origin. Mortalities included returns from fisheries and salmon whose final telemetry records were outside spawning tributaries, usually between dams. We felt that these operational definitions represented the true fates of fish for several reasons. First, the spatial distribution of spawning habitat of sockeye in the Columbia basin is highly restricted relative to other salmon species (Mullan 1986; Groot and Margolis 1991; McClure et al. 2003). Hence, successful spawning in unmonitored tributaries or the mainstem Columbia River was unlikely. Second, the rate of transmitter loss through regurgitation was low (<1%, $n = 3$), a similar rate observed in other studies (Ramstad and Woody 2003; Keefer et al. 2004*a*) and these fish were not considered in further analyses. Third, the linear nature of the study system and large number of receivers used (Table 1) provided a high probability of detection, particularly at dams. For instance, we estimate the probability of a fish last recorded in the Hanford Reach reaching a spawning tributary by passing the next two dams undetected at $<1.0 \times 10^{-7}$ based on the minimum number of fixed site receivers that salmon passed at these dams ($n = 8$) and frequencies of receiver outage at these sites (mean outage = 14.0%, SD = 6.0%). Thus, while many fish went undetected at individual antennas, it was improbable that misclassification of fates seriously biased our results overall.

Reach survival estimates

In addition to overall survival to spawning tributaries, we estimated survival through each hydrosystem segment. Reach-specific survival (S_i) was calculated with the formula

$$S_i = (N_{i+1} + T_i)/N_i$$

where N_{i+1} is the number of fish that passed the upstream dam, T_i is the number of fish that entered spawning tributaries in the reach above dam *i*, and N_i is the number of fish that passed the downstream dam. Fish that passed the dam at the upstream end of a reach were considered to have survived through the reach regardless of subsequent downstream movement. Fish last recorded in tributaries downstream from known spawning habitat (all tributaries downstream from

Table 1. Location of receivers at dams and tributaries with number of antennas and percent time in operation in 1997.

Receiver site	Receiver location	No. of antennas	% time in operation
Bonneville Dam	Tailrace	2	95.5
	Dam	68	92.5
	Ladder	33	96.2
	Navigation lock	5	96.6
The Dalles Dam	Tailrace	2	89.9
	Dam	6	97.9
	Ladder	15	96.9
John Day Dam	Tailrace	2	98.7
	Dam	3	99.9
	Ladder	17	94.8
McNary Dam	Tailrace	2	91.7
	Dam	38	94.5
	Ladder	17	96.8
	Navigation lock	6	98.8
Priest Rapids Dam	Tailrace	2	84.8
	Dam	22	93.4
	Ladder	13	85.2
Wanapum Dam	Tailrace	2	82.8
	Dam	18	96.3
	Ladder	12	95.3
Bridge of the Gods	Bonneville Dam forebay	1	96.2
Wind River	Mouth	1	93.6
Little White Salmon River	Mouth	1	94.1
White Salmon River	Mouth	1	88.9
Hood River	Mouth	1	98.3
Klickitat River	Mouth	1	97.3
Deschutes River	Mouth	1	98.7
John Day River	Mouth	1	85.3
Umatilla River	Mouth	1	99.9
Walla Walla River	Mouth	1	97.8
Yakima River	Mouth	1	95.7
Hanford Reach	Right and left banks	2	88.3

Rock Island Dam) were considered strays that did not survive to spawning areas.

Passage time calculations

We used tailrace and top-of-ladder sites for calculating dam and reservoir passage times. Dam passage times were calculated from the first record at a tailrace receiver (0.5–3.2 km downstream from dams) to the last record at a top-of-ladder receiver. Some fish migrated back out of tailraces, a behavior that we believe was related to route searching or unfavorable passage conditions at dams, and dam passage times included this time. Reservoir passage times were calculated from the last top-of-ladder record at the downstream dam to the first tailrace record at the upstream dam of each reservoir. Reservoir passage times were converted to daily rates using river kilometres because reservoir lengths varied. Time that sockeye salmon temporarily strayed into tributaries was included in total reservoir passage time, but did not include time fish spent downstream from dams after fallback events (downstream movement through turbines, juvenile bypass facilities, fish ladders, or navigation locks or over spillways; Reischel and Bjornn 2003). Sample sizes for dam passage and reservoir migration times varied between sites because of mortalities between dams and loss of receiver coverage resulting primarily from power outages or vandalism. In particular, we could not calculate passage times for 254 fish at McNary Dam (64% of all passages) or 259 fish at Priest Rapids Dam (60% of all passages), because they were recorded near top-of-ladder sites but missed the uppermost antennas because of receiver outages.

Environmental data and statistical analysis

We performed statistical analyses to assess the relationships between migration performance and behavior and environmental variables at several scales. First, we used binary logistic regression (Hosmer and Lemeshow 1999) to test whether environmental conditions, relative migration speed, or fallback history was associated with migration success. Prior to the regression analysis, we used principal components analysis (PCA) to summarize variation in five predictors because of strong intercorrelation among environmental predictors. The PCA included mean daily temperature and discharge at Bonneville Dam on the day of tagging and tagging date as a potential cue signaling the end of the spawning season (pairwise Pearson's $r^2 = 0.620–0.897$, $p \leq 0.001$) (e.g., Fig. 2). Mean relative passage times and migration rates were used to estimate the relative migration speed in the lower Columbia River among sockeye salmon and were estimated by taking the mean of the normal deviates (Zar 1999) for passage time or migration rate through each lower Columbia River project. The PCA scores for each fish were then used as predictors in the logistic regression model. The fallback history of each fish was included as an additional categorical predictor by classifying fish as having fallen back over one or more dams or not. A Hosmer–Lemeshow test tested the goodness-of-fit of the logistic regression model to the data using the "smart = 10" option in Systat v.10 (Steinberg and Colla 1997). We used the mean daily flow and temperature at the time the fish first entered each dam tailrace obtained from the US Army Corps of Engineers (compiled by the University of Washington at http://www.cqs.washington.edu/dart/dart.html). No interaction terms were significant in preliminary models ($p > 0.10$) and were subsequently excluded.

At a finer scale, we examined migration behavior at dams and through reservoirs in relation to daily and seasonal variation in environmental conditions. We used event-time analysis (also known as survival or failure-time analysis; Hosmer and Lemeshow 1999; Castro-Santos and Haro 2003) to examine the relationship between passage time at each dam and predictor variables describing environmental conditions and fish traits. A Cox proportional hazards regression model in the form

$$h_{i(t)} = \lambda_0(t)\exp[\beta_1 x_{i1} + \ldots + \beta_k x_{ik}(t)]$$

where $h_{i(t)}$ is the probability or "hazard" of passage of individual i at time t, given that an individual had not passed prior to time t. The model relates individual hazards to a baseline hazard function $\lambda_0(t)$, which is left unspecified. The model then fits a set of regression coefficients β_{ij} by maximum likelihood using a set of predictor covariates $x_{i1},..., x_{ij}$ describing environmental conditions and fish traits for each fish, and these covariates may be constant (e.g., fish length at tagging) or time varying (e.g., light level at the time of passage). The Cox proportional hazards models have several advantages over traditional analysis of variance (ANOVA) approaches or other event-time models (Allison 1995; Castro-Santos and Haro 2003). First, individuals that are recorded at the tailrace of a dam but that do not pass can be explicitly included in the modeling. These individuals are modeled as "at risk of passage" at the time of tailrace detection and remain in the risk set until censoring, as described below. Second, the covariates may vary through time, allowing passage hazards to change daily or seasonally. The primary disadvantage is that the models are semiparametric in the sense that hazards are calculated using the ranks of covariate values, and consequently, quantitative differences among treatments cannot be modeled as in traditional regression (Allison 1995; Castro-Santos and Haro 2003). Hazard ratios compare the probability of the event occurring within a given time interval for an individual belonging to one group versus another (e.g., females versus males) or for an increase in one unit of a continuous predictor variable. The models included the length of each fish at the time of tagging as a measure of body size, fish sex, and two time-varying covariates: the date of passage and time of day, a binary variable coding for day versus night. The date of passage for each fish at each project was used as a compound measure of seasonal changes in temperature and discharge and as a predictor of seasonal effects on migration behavior owing to the high intercorrelations among these variables as indicated by unstable parameter estimates and extremely large standard errors in models incorporating multiple environmental predictors (unpublished analyses; Allison 1995). Models replacing passage date with mean daily discharge, spill, or temperature produced qualitatively identical results. The daily time of switching between day and night was estimated using sunrise–sunset times at Stevenson, Washington, obtained from the US Naval Observatory (http://aa.usno.navy.mil/data/docs/RS_OneYear.html), because passage is known to slow substantially at night (Quinn and Adams 1996) (see Results) and to account for changes in day length during the run. All proportional hazards regressions were performed using SAS v.8e (SAS Institute Inc., Cary, N.C.) with the efron option for breaking ties (Allison 1995). Fish were censored if they (*i*) were detected at the tailrace antenna but did not pass the dam, (*ii*) passed the dam (i.e., they were detected upstream) but were not detected at the top-of-ladder antenna, or (*iii*) passed via the navigation lock. We used data from other dam antennas to assign censoring times (the time when fish were lost to followup) or, when unavailable, the censoring time equaled the maximum observed passage time. Reported p values are uncorrected for multiple comparisons across dams.

For the event-time models, we focused on the relationship between passage time (as modeled by hazard of passage) and predictor variables at individual dams because of the potential importance of passage facilities at each hydroelectric project in the management of this species. We also used a repeated-measures, mixed-model ANOVA followed by a series of contrasts to examine whether mean passage times differed among hydroprojects. The repeated-measures model related the mean passage time observed at each dam to migration success, the date of tagging, and the time of day that fish entered the tailrace of the dam because there was a strong diel periodicity observed in passage behavior (see Results). We then used contrasts to test (*i*) whether mean passage times differed at lower versus mid-Columbia River projects and (*ii*) whether mean passage time differed among dams within region. All dam passage time analyses were restricted to first passage attempts (i.e., excluding fallback time) and excluded known hatchery (clipped) fish. Passage times were $\log_e$-transformed to improve normality and homogeneity of the error terms.

We assessed the rate of migration through reservoirs and the Hanford Reach using a similar repeated-measures ANOVA model and contrasts. An additional contrast tested whether migration rates through the Hanford Reach differed from those through all reservoirs. The appropriateness of four different covariance structure types (unstructured, compound symmetric, autoregressive, and heterogeneous autoregressive) was compared for both the passage time and the migration rate ANOVA models using the Akaike information criterion (Burnham and Anderson 2002); these comparisons suggested improvements in model fit using a heterogeneous autoregressive structure in both cases.

We compared the proportion of time successful migrants spent passing dams, ascending reservoirs, passing the Hanford reach, or in other activities (e.g., reascending dams after fallback) for 12 fish that had complete records at all tailrace and top-of-ladder antennas. A Freidman test was used to test for differences in mean proportions (Zar 1999). Qualitatively identical results were obtained using records of fish (n = 90) that passed Rock Island Dam, had complete passage time records at four or more dams, but were not detected at one of the 20 tailrace or top-of-ladder receivers required to record a complete record. The fallback rate for the sockeye salmon among complete-record fish (25.0%, n = 12) was nearly identical to that for all fish (25.6%, n = 574).

Results

Patterns of survival, straying, and migratory timing

Approximately two thirds of the radio-tagged sockeye salmon reached spawning tributaries (Table 2). About 41% of the fish that passed Rock Island Dam entered tributaries of Lake Wenatchee. Most of the fish passing Wells Dam (n = 231) were last recorded in the Okanogan River. Approximately 11% (n = 65) of the radio-tagged sockeye salmon were reported as harvested in mainstem Columbia River fisheries. Sockeye salmon with last records at a mainstem dam or reservoir comprised 18% (n = 100) of all radio-tagged fish; these fish presumably represent nonfisheries mortality. Reach survival estimates for sockeye salmon in 1997 exceeded 90% through all sampled reaches in the Columbia River hydrosystem except for the reach between Bonneville and The Dalles dams (87.4%) (Table 2).

Sockeye salmon took approximately 3 weeks to pass through the Columbia River hydrosystem. The migratory timing of the Wenatchee and Okanogan River stocks did not differ (Kolmogorov–Smirnov two-sample test, p = 0.52). Sockeye salmon that returned to these drainages were radio-tagged at Bonneville Dam primarily from mid-June to mid-July with median tag dates of 29 June for both stocks. Although the sample size was small (n = 10), fish bound for the White River drainage (Wenatchee River tributary) passed Bonneville Dam from late June through mid-July (median tag date 3 July). Median passage date at Rock Island Dam was 18 July (range 2 July – 16 August) with a median time of 20 days after tagging. Median arrival dates upstream at Wells Dam were 2 days later for Methow and Okanogan River stocks (20 July, range 5 July – 18 August).

Migration success was related to both seasonal environmental variation and relative migration speed. The PCA of variation in environmental variables and two measures of relative migration speed produced two axes corresponding primarily to variation in date, discharge, and temperature (axis 1, season) and relative migration rate in the lower Columbia (axis 2, speed) (Table 3). The fate of each fish was significantly related to both of these summary predictor variables. Adults that entered late and that encountered lower flows and higher temperatures were less successful. Relatively slow migration rates (slow migration through reservoirs and long passage times at dams in the lower Columbia; Table 3) were also associated with unsuccessful migration. The strong intercorrelations between tagging date and environmental factors made it impossible to relate variation in migration success to environmental factors versus phenological changes in behavior among individuals within the run. Migration success was marginally significantly related to fallback history (Table 4). Contrary to expectation, adults that fell back were more likely to successfully migrate. The Hosmer–Lemeshow test suggested that the model was an adequate description of the data ($H\text{–}L_{df8} = 6.062$, p = 0.640) and correctly classified the fate of 70.4% of the fish. Most notably, only a single salmon of 27 (3.7%) tagged at Bonneville Dam during the period 24 July – 5 August successfully reached a spawning tributary (Fig. 4), concomitant with the onset of stressful river temperatures. In comparison, 61.3% of salmon tagged during the period 5–16 July were successful migrants (n = 155).

Passage of dams, reservoirs, and the Hanford Reach

We used ANOVA and proportional hazards regression to test for relationships between passage time and fish traits, environmental conditions, and fate at two scales: throughout migration and at individual dams. Passage times differed among most dams within region and were longer at mid-Columbia than at lower Columbia River dams (Fig. 5; Table 5). Distributions of passage times at all dams were skewed because some fish had long passage times, with 2%–8% taking 5 days or more to pass (Fig. 5). Mean passage times at dams decreased significantly during the migration season when assessed across dams (Fig. 6; Table 6), concomitant with increasing temperatures.

When statistically controlling for variation among individuals, dams, season, and arrival date at the tailrace (Table 5), the mean passage time of unsuccessful migrants was 13.7% slower than that of successful migrants based on back-transformed means (mean successful = 17.8 h, mean unsuccessful = 20.3 h). In contrast, the effect of fate was not significant at any of the dams except Bonneville Dam in the partial hazards regressions (Table 6), suggesting a cumulative effect of slow passage on migration success.

There was a strong diel periodicity in passage times (Fig. 7), and the time of arrival at the tailrace affected passage time because only about 10% of sockeye salmon passed top-of-ladder receivers at dams at night (2100–0500) (Fig. 8). Consequently, within a given time interval, the probability of passage at night was 0.093–0.308 that of passage during the day, i.e., passage during the day was 3.24–10.7 times more likely than at night (Fig. 7; Table 6). Additionally, passage hazard ratios declined with fish size, corresponding to faster passage times in larger fish at one lower Columbia and three out of four mid-Columbia projects. Sex was not related to passage hazard at any location (Table 6).

Migration rates in reservoirs were also related to seasonal changes in conditions as measured by tagging date and to migration success. Rates were rapid, ranging from mean rates of 37.8 km·day^{-1} at the Rock Island Reservoir to 61.3 km·day^{-1} at the John Day Reservoir (Fig. 9), and sockeye salmon migrated more rapidly through lower Columbia River reservoirs than through mid-Columbia River reservoirs, with mean rates 10.7–24.4 km·day^{-1} faster through lower Columbia reservoirs (Table 7; Fig. 9). Most pairwise comparisons within region were significantly different (Table 7). Overall mean reservoir migration rate was 3.3 km·day^{-1} (7.25%) higher in successful migrants than in unsuccessful migrants, primarily because of a decrease in migration rate in late-season, unsuccessful migrants (Table 7;

Table 2. Fate and reach survival estimates for sockeye salmon released downstream from Bonneville Dam in 1997.

Reach			Survived in reach (%)			Did not survive in reach (%)				Cumulative (%)	
Downstream	Upstream	Entered reach	Passed upstream dam	Spawning tributary	Total	Mainstem harvest	Stray	Unknown	Total	Survival	Mortality
Bonneville	The Dalles	563	87.4 (492)		87.4	9.2 (52)	0.9 (5)	2.5 (14)	12.6	87.4	12.6
The Dalles	John Day	492	95.1 (468)		95.1	1.0 (5)[a]	0.6 (3)[b]	3.3 (16)	4.9	83.2	16.8
John Day	McNary	468	97.6 (457)		97.6		0.2 (1)[c]	2.1 (10)	2.4	81.2	18.8
McNary	Priest Rapids	457	94.7 (433)		94.7	1.8 (8)	0.2 (1)	3.3 (15)	5.3	76.9	23.1
Priest Rapids	Wanapum	433	98.6 (427)		98.6			1.4 (6)	1.4	75.8	24.2
Wanapum	Rock Island	427	97.9 (418)		97.9			2.1 (9)	2.1	74.2	25.8
Rock Island	Rocky Reach	418	57.4 (240)	41.4 (173)	98.8			1.7 (5)	1.2	73.4	26.6
Wenatchee River				(163)							
White River				(9)							
Napeequa River				(1)							
Rocky Reach	Wells	240	96.3 (231)	1.7 (4)	97.9			2.1(5)	2.1	72.5	27.5
Entiat River				(1)							
Wenatchee River[d]				(3)[d]							
Wells	Chief Joseph	231	na	91.3 (211)	91.3			8.7(20)	8.7	68.9	31.1
Methow River				(3)							
Okanongan River				(208)							
Fate totals				68.9 (388)		11.5 (65)	1.8 (10)	17.8 (100)		68.9	31.1

Note: “Entered reach” indicates that fish passed the downstream dam. Sample sizes are given in parentheses. na, not available.
[a]One fish fell back over The Dalles Dam and was captured in a tribal fishery downstream from The Dalles Dam.
[b]Fell back over The Dalles Dam and entered tributaries downstream from The Dalles Dam.
[c]Fish fell back over The Dalles and John Day dams and entered a tributary downstream from The Dalles Dam.
[d]Three fish fell back at Rocky Reach Dam and entered the Wenatchee River downstream from Rocky Reach Dam.

Table 3. Component loadings from PCA of variation in tagging date, temperature, and discharge at Bonneville Dam on the date of tagging and relative passage time and migration rate through the lower Columbia River hydrosystem.

Factor	PCA1 (season)	PCA2 (speed)
Tag date	0.962	0.214
Temperature	–0.937	–0.023
Discharge	0.919	0.284
Relative passage time	–0.319	0.723
Relative migration rate	0.410	–0.628
% of variance explained	54.1	25.2

Table 4. Results of multiple logistic regression test for relationships between probability of successful migration and seasonal changes in environmental conditions, relative migration speed, and fallback history.

Parameter	Estimate	SE	*t* ratio	*p*
Constant	1.561	0.149	10.500	<0.001
PCA1 (season)	–0.721	0.120	–6.035	<0.001
PCA2 (speed)	0.468	0.118	3.969	<0.001
Fallback history	0.497	0.255	–1.945	0.052

Fig. 4. Histogram representing the number of sockeye salmon tagged by date for successful (solid bars) and unsuccessful migrants (open bars).

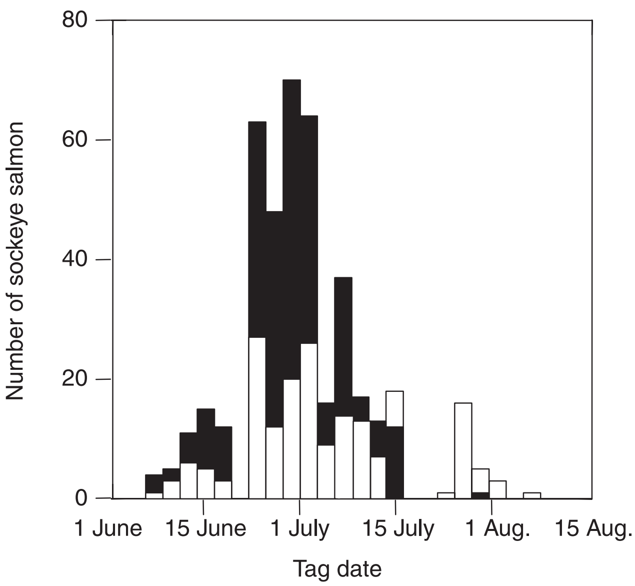
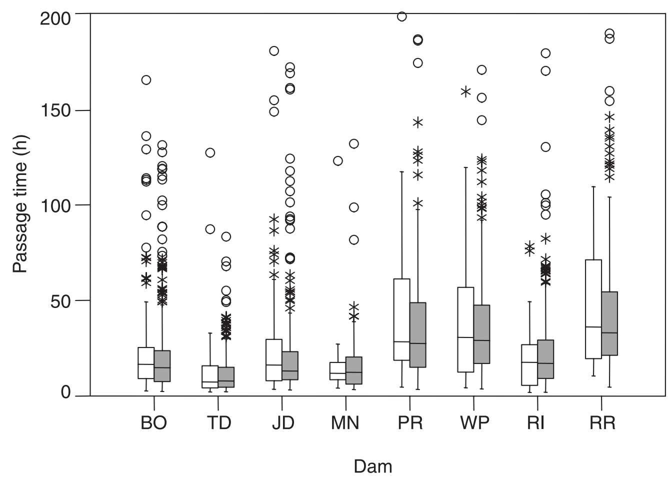


Fig. 10). Salmon ascended the unimpounded Hanford Reach at a slower rate (mean = 26.9 km·day^{-1}) than they did reservoirs (Table 7; Fig. 9). Radio-tagged sockeye salmon arrived at the lower Hanford receivers and at receivers at the upper ends of reservoirs throughout the day and night in 1997 (Fig. 8), suggesting frequent movement within reservoirs at night. In contrast, first records at the upper end of the Hanford Reach were more frequent during daylight hours.

Fig. 5. Passage times at each dam for successful (shaded boxes) and unsuccessful (open boxes) migrating sockeye salmon. Passage times >200 h are excluded for clarity: five fish for Bonneville (216–402 h), two fish for John Day (294 and 316 h), six fish for Priest Rapids (231–448 h), four fish for Wanapum (216–402 h), three fish for Rock Island (207–243 h), and one fish for Rocky Reach (344 h). Dam abbreviations: BO, Bonneville; TD, The Dalles; JD, John Day; MN, McNary; PR, Priest Rapids; WP, Wanapum; RI, Rock Island; RR, Rocky Reach. Asterisks (*) represent outliers and circles represent extreme outliers.



Hydrosystem passage times

Passage times and rates through longer hydrosystem reaches integrated multiple dam and reservoir passages and time fish spent falling back over and reascending dams. Passage times for 189 sockeye salmon from the Bonneville Dam tailrace to pass McNary Dam (four dams, three reservoirs, 238 km) ranged from 4.0 days (59.5 km·day^{-1}) to more than 29 days (8.2 km·day^{-1}) with a median time of 6.8 days (34.5 km·day^{-1}). Passage times for 178 sockeye salmon from Bonneville Dam past Priest Rapids Dam (five dams, four reservoirs, Hanford Reach, 407 km) ranged from 8.5 days (47.9 km·day^{-1}) to more than 30 days (13.6 km·day^{-1}) (median = 12.9 days, 31.5 km·day^{-1}). Median passage times were 17.3 days (28.7 km·day^{-1}) for 397 sockeye salmon from the Bonneville Dam tailrace past Rock Island Dam (seven dams, six reservoirs, Hanford Reach, 497 km) and 19.0 days (27.9 km·day^{-1}) for 212 fish from Bonneville Dam past Rocky Reach Dam (eight dams, seven reservoirs, Hanford Reach, 530 km).

Salmon with complete migration records spent similar proportions of time passing dams and ascending reservoirs (dams: 36.6%, 31.3%–41.9%; reservoirs: 43.1%, 38.2%–48%; mean and 95% confidence interval) (Fig. 11). Salmon spent nearly one fifth of their total migration time ascending the Hanford Reach (17.9%, 15.7%–20.2%; Friedman test $F_F = 32.80$, df = 3, $p < 0.001$, $n = 12$), nearly identical to the proportion of the total monitored migration distance that this river section represents (17.1%). Other activities such as time spent falling back over and reascending dams accounted for a small proportion of time (2.4%, 0%–5.1%).

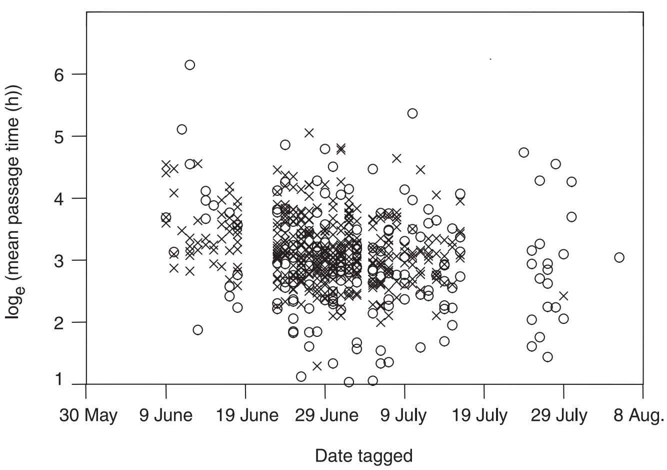
Table 5. Results of repeated-measures ANOVA testing for differences in $\log_e$(mean passage time) at dams and contrasts testing for differences between lower versus mid-Columbia River dams and among dams within river region.

Effect	Numerator df	Denominator df	*F*	*p*
Fate	1	551	4.65	0.0314
Dam	7	1933	52.25	<0.0001
F1 hour[a]	23	1735	2.47	0.0001
Tag date	1	551	44.96	<0.0001
Dam × fate	7	1933	1.75	0.0934
Contrast				
LC versus MC	1	1933	163.32	<0.0001
BO versus TD	1	1933	86.08	<0.0001
BO versus JD	1	1933	0.41	
BO versus MN	1	1933	5.31	
TD versus JD	1	1933	82.64	<0.0001
TD versus MN	1	1933	10.7	
JD versus MN	1	1933	7.29	
PR versus WP	1	1933	1.53	
PR versus RI	1	1933	47.43	<0.0001
PR versus RR	1	1933	0.04	
WP versus RI	1	1933	41.86	
WP versus RR	1	1933	1.79	
RI versus RR	1	1933	46.26	<0.0001

Note: Dam abbreviations: LC, lower Columbia River dams; MC, mid-Columbia River dams; BO, Bonneville; TD, The Dalles; JD, John Day; MN, McNary; PR, Priest Rapids; WP, Wanapum; RI, Rock Island; RR, Rocky Reach.

[a]F1 hour is the hour that sockeye salmon first arrived at the dam tailrace.

Fig. 6. Passage time at all dams in relation to date of tagging at Bonneville Dam for successful (crosses) and unsuccessful migrants (circles). The median untransformed passage time was 17.1 h (range 2.0–480.0 h).



Discussion

During the high-water year of 1997, approximately two thirds of tagged sockeye salmon successfully migrated past seven or nine dams in the Columbia River hydrosystem to reach spawning tributaries. Most striking was the decline in survival during the late portion of the run as flows decreased and temperatures increased. Notably, migration success was related to overall migration speed — unsuccessful migrants exhibited slow passage of dams and reservoirs, although this effect appeared to be scale dependent because the relationship between passage time and fate was not significant at most dams. General examination of migration revealed that migration was faster in the lower Columbia and quickened through the migration season. Dam passage and migration through the Hanford Reach were slower and displayed greater diel periodicity compared with migration in reservoirs. Below, we discuss potential mechanisms that could generate these patterns and implications for management, first at the hydrosystem scale and then at the finer scale of individual reaches.

Patterns of migratory timing and survival

The majority of radio-tagged sockeye salmon reached spawning tributaries and survival estimates were comparable with those reported for other Columbia River salmonids (Dauble and Mueller 2000). Dam counts are the primary method of estimating survival of adult salmon between hydroelectric projects, although several potential sources of error contribute to uncertainty in survival estimates (Dauble and Mueller 2000). To our knowledge, there have been no direct estimates of system-wide survival for individual Columbia River sockeye salmon runs prior to this study. We believe that survival estimates derived from telemetry studies are more reliable than those calculated from dam counts or passive integrated transponder tagging because they track individual fish, account for fallback, can better partition known and unaccounted-for loss factors including straying and fisheries take, and provide greater resolution to detect patterns such as the seasonal decline in survival observed here.

Table 6. Results of Cox proportional hazards regression test of passage hazard at each dam.

Dam	Variable	df	Parameter estimate	SE	χ^2	*p*	Hazard ratio
Bonneville (event = 502, censored = 52)	Fate	1	0.2679	0.1049	6.5234	0.0106	1.3070
	Time of day	1	–2.3530	0.1908	152.0245	<0.0001	0.0950
	Passage date	1	–0.0001	0.0044	0.0006	0.9813	1.0000
	Fork length	1	0.0092	0.0155	0.3535	0.5521	1.0090
	Sex	1	0.0495	0.1004	0.2436	0.6216	1.0510
The Dalles (event = 414, censored = 5)	Fate	1	0.1489	0.1326	1.2610	0.2615	1.1610
	Time of day	1	–1.4488	0.1537	88.8311	<0.0001	0.2350
	Passage date	1	0.0060	0.0052	1.3517	0.2450	1.0060
	Fork length	1	–0.0038	0.0164	0.0533	0.8174	0.9960
	Sex	1	0.1405	0.1137	1.5269	0.2166	1.1510
John Day (event = 341, censored = 26)	Fate	1	0.2685	0.1495	3.2247	0.0725	1.3080
	Time of day	1	–1.9914	0.2266	77.2051	<0.0001	0.1370
	Passage date	1	0.0185	0.0061	9.2286	0.0024	1.0190
	Fork length	1	0.0065	0.0169	0.1489	0.6996	1.0070
	Sex	1	–0.0164	0.1214	0.0182	0.8926	0.9840
McNary (event = 141, censored = 419)	Fate	1	0.1932	0.2467	0.6135	0.4335	1.2130
	Time of day	1	–2.3802	0.3693	41.5426	<0.0001	0.0930
	Passage date	1	–0.0348	0.0132	6.9467	0.0084	0.9660
	Fork length	1	–0.0741	0.0311	5.6826	0.0171	0.9290
	Sex	1	–0.1968	0.1903	1.0695	0.3011	0.8210
Priest Rapids (event = 175, censored = 255)	Fate	1	0.1501	0.2377	0.3989	0.5277	1.1620
	Time of day	1	–1.2425	0.2154	33.2671	<0.0001	0.2890
	Passage date	1	–0.0221	0.0104	4.5761	0.0324	0.9780
	Fork length	1	–0.0145	0.0270	0.2898	0.5904	0.9860
	Sex	1	0.1201	0.1653	0.5273	0.4677	1.1280
Wanapum (event = 381, censored = 12)	Fate	1	–0.0062	0.1846	0.0011	0.9734	0.9940
	Time of day	1	–1.4565	0.1659	77.0916	<0.0001	0.2330
	Passage date	1	–0.0312	0.0072	19.0141	<0.0001	0.9690
	Fork length	1	–0.0402	0.0160	6.3131	0.0120	0.9610
	Sex	1	0.0406	0.1134	0.1283	0.7202	1.0410
Rock Island (event = 371, censored = 17)	Fate	1	–0.1465	0.2119	0.4778	0.4894	0.8640
	Time of day	1	–1.1790	0.1390	71.9670	<0.0001	0.3080
	Passage date	1	0.0030	0.0073	0.1727	0.6777	1.0030
	Fork length	1	–0.0438	0.0179	5.9897	0.0144	0.9570
	Sex	1	0.2453	0.1163	4.4497	0.0349	1.2780
Rocky Reach (event = 206, censored = 21)	Fate	1	0.1022	0.2430	0.1769	0.6741	1.1080
	Time of day	1	–1.5761	0.2227	50.0677	<0.0001	0.2070
	Passage date	1	–0.0641	0.0112	32.6743	<0.0001	0.9380
	Fork length	1	–0.0616	0.0299	4.2380	0.0395	0.9400
	Sex	1	0.1089	0.1603	0.4613	0.4970	1.1150

Individual sockeye salmon migration success was strongly related to arrival date at Bonneville Dam. We used the date of tagging as a summary measures because river discharge, spill levels at dams, river temperature, and date were all intercorrelated, preventing us from partitioning patterns in survival to these potential causes in a rigorous manner. Nonetheless, temperature was probably the primary factor affecting migration success. Elevated water temperatures during upstream migration have been linked to higher in-river and prespawning mortality of sockeye salmon in the Columbia Basin (Major and Mighell 1967) and the Fraser River (Gilhousen 1990; Macdonald et al. 2000; Cooke et al. 2004). Adult exposure to elevated temperatures can increase susceptibility to disease and compromise reproductive performance (Coutant 1999; Torgersen et al. 1999) through increased metabolic demands (Rand and Hinch 1998), reduced allocation to gonadal development (Kinnison et al. 2001), and reduced egg viability (Berman and Quinn 1991). Extended exposure of adult salmonids to water temperatures >18 °C may increase the risk of prespawning mortality (mortality after adults have reached spawning tributaries; Becker and Fujihara 1978; Gilhousen 1990), and temperatures above 24 °C are lethal (Servizi and Jensen 1977). Cooke et al. (2004) identified several mechanisms that may have contributed to the dramatic in-river and prespawn mortality observed in late-run sockeye salmon in the Fraser River since 1995. While underlying causes of mortality are still unclear in the Fraser River, it is likely that temperature plays a direct or indirect role because the high mortality has been observed in a portion of the run entering the river more

Fig. 7. Passage time of sockeye salmon at individual dams in relation to the hour of first detection at the tailrace receiver. Observations are blocked by the number of nights elapsed between the first detection and subsequent passage. Numbers of nights at individual dams are zero (○), one (×), two (+), three (△), and four (▽). Passage times were longer for salmon arriving under cover of night compared with those arriving during the day, within nights at dam.

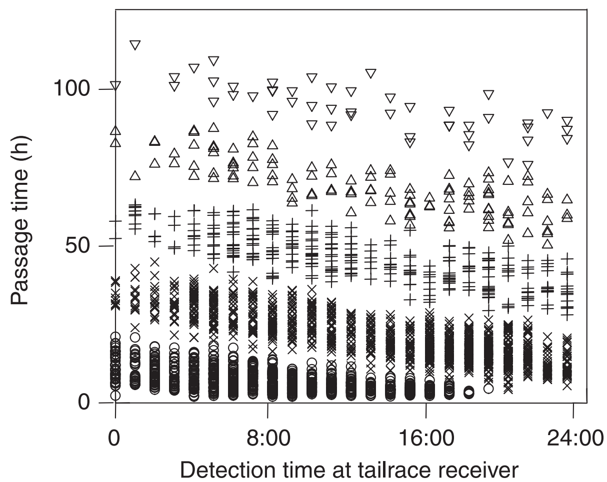


Fig. 8. (*a*) Diel pattern of records at the upper end of reservoirs and base of dams, (*b*) time of exit from top-of-ladder, (*c*) time at the downstream end of Hanford Reach, and (*d*) time at the upstream end of the Hanford Reach.

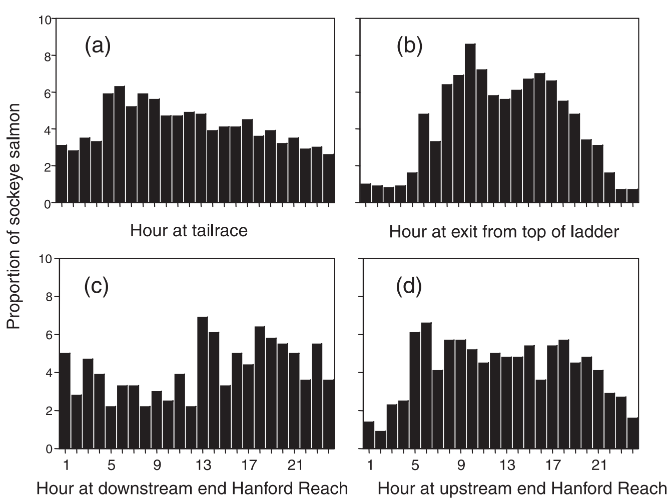
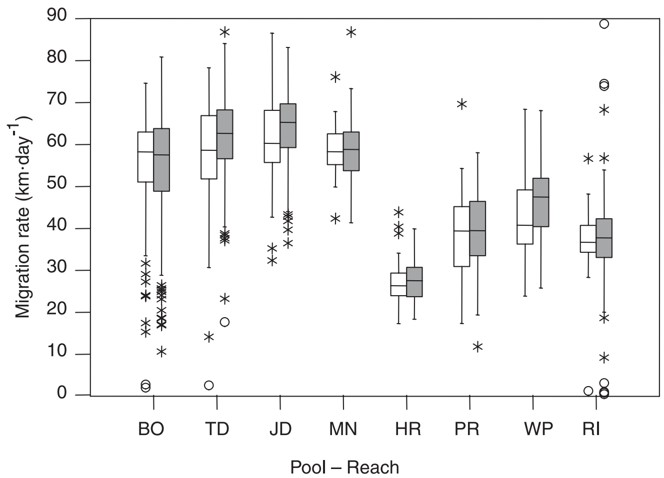


Fig. 9. Migration rate through reservoirs and Hanford Reach in relation to eventual fate of each sockeye salmon. Open boxes represent unsuccessful migrants and shaded boxes represent successful migrants. Pool and reach abbreviations: BO, Bonneville; TD, The Dalles; JD, John Day; MN, McNary; HR, Hanford Reach; PR, Priest Rapids; WP, Wanapum; RI, Rock Island. Asterisks (*) represent outliers and circles represent extreme outliers.



than 6 weeks earlier in the season than the historical pattern, shifting migration to a period of warmer water temperatures in August (Cooke et al. 2004). In our study, the precipitous drop in migration success occurred for sockeye salmon tagged after the second week of July as temperatures at Bonneville Dam and elsewhere in the drainage exceeded 20 °C.

The pattern of mortality that we observed could have been caused by other measured or unmeasured factors or may have arisen through a temperature-dependent tagging effect. Unfortunately, we could not determine the relationship between temperature and any handling effects with our study design, although several lines of evidence suggest a minimum handling effect. First, there was no mortality during tagging, transport, or release. Second, while both sources of mortality would contribute to the decline in migration success late in the season, telemetry data indicated that the tagged fish in the late period did not die immediately after release, with most fish passing two or more dams and living a week or more post-tagging during the late period. While both sources of mortality would produce a similar pattern of migration success, these data indicate that the tagged fish in the late period did not die immediately after release. Finally, we estimated survival for sockeye salmon migrating during these two periods using dam count data from Bonneville and Rock Island dams and assuming a 16-day passage time between these dams (the mean migration time observed for sockeye salmon tagged on 4–16 July). Although these estimates have several potential sources of error, a large decline in survival was also observed in the dam count sample, with estimated migration success dropping from 94.2% to 56.3% later in the summer. Taken together, ancillary evidence suggests that tag and handling effects were not the primary cause of the decline in survival that we observed. In addition, the seasonal pattern of mortality could not be attributed to changes in seasonal fishing pressure: only 2 of 65 fish reported captured in tribal fisheries were tagged during the late period.

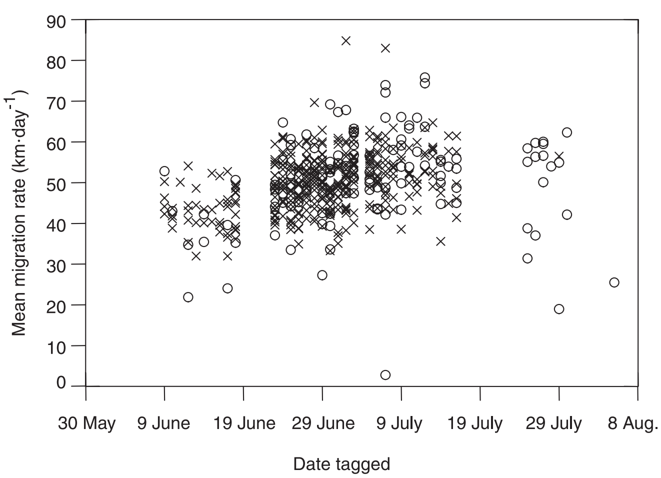
Several mechanisms may have contributed to the observed relationships among migration success, speed, and season. First, the relationship between migration success and speed could be direct, where slowed migration caused by dams resulted in the expenditure of energy that slowed migration at upstream projects and subsequently lowered the probability of successful migration. Alternatively, slow migration may have resulted from poor initial physiological condition leading to slowed migration, increased thermal exposure, and subsequent low probability of migration success. These two mechanisms are not mutually exclusive and rather would likely work synergistically to decrease migration success.

Table 7. Results of repeated-measures ANOVA and contrasts for the effects of season on migration rates among reaches.

Effect	Numerator df	Denominator df	F	p
Fate	1	492	20.87	<0.0001
Dam	7	1607	274.41	<0.0001
Tag date	1	492	81.96	<0.0001
Dam × fate	7	1607	1.71	0.0992
Contrast				
LC (n = 3) versus MC (n = 4)	1	1607	686.86	<0.0001
Hanford Reach versus all reaches	1	1607	1047.65	<0.0001
BO versus TD	1	1607	30.52	<0.0001
BO versus JD	1	1607	75.04	<0.0001
BO versus MN	1	1607	6.44	0.0113
TD versus JD	1	1607	15.49	<0.0001
TD versus MN	1	1607	1.17	0.2789
JD versus MN	1	1607	14.75	0.0001
PR versus WP	1	1607	26.22	<0.0001
PR versus RI	1	1607	3.91	0.0482
WP versus RI	1	1607	63.54	<0.0001

Note: Reach abbreviations: LC, lower Columbia River dams; MC, mid-Columbia River dams; BO, Bonneville; TD, The Dalles; JD, John Day; MN, McNary; PR, Priest Rapids; WP, Wanapum; RI, Rock Island.

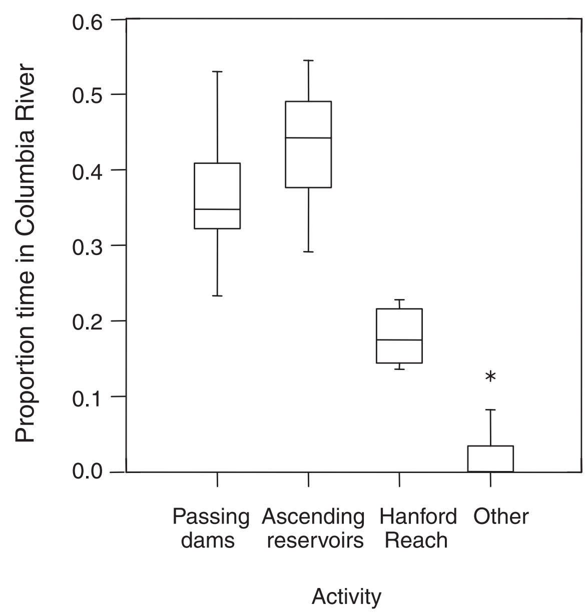
Fig. 10. Migration rate in relation to date of tagging for successful (crosses) and unsuccessful (circles) migrating sockeye salmon.



Notably, the seasonal pattern of mortality may have been related to both factors. It is plausible that late-entry fish were in relatively poor initial physiological state, perhaps having delayed entry to continue ocean feeding, and this subsequently led to poor initial condition, slow migration rates, increased thermal exposure, and low migration success. Clearly, understanding the relationship between initial condition and migration success is important in a management context because the relative importance of each mechanism will determine the effectiveness of management actions aimed at improving passage conditions at dams — efforts to improve passage at dams will provide little benefit if migration success is primarily related to fish condition at river entry.

Regardless of mechanism, the observed pattern of seasonal mortality suggests the potential for current selection on run timing. The upstream migration of anadromous salmonids is an energetically demanding part of the life cycle and its initiation is largely governed by the interactions of water temperature, flow regime, and other factors that influence maturation (Gilhousen 1990; Hodgson and Quinn 2002). Substantial variation exists in the timing of spawning migrations of North American sockeye salmon populations and is thought to relate to temporal variation in both migration conditions for adults and spawning and rearing conditions in

Fig. 11. Proportion of total migration time from the Bonneville Dam tailrace to the tailrace at Rock Island Dam that sockeye salmon recorded during first passages over dams, ascending reservoirs, ascending the Hanford Reach, or other activities including second passage times for salmon that fell back at dams. Analysis was limited to fish with complete passage records at five or six of the first six dams and in the Hanford reach (n = 90, including six fish that were not recorded in one of the spawning tributaries). Asterisk represents outlier.



tributaries (Tagaki and Smith 1973; Merritt and Roberson 1986; Hodgson and Quinn 2002). For example, Columbia River and interior British Columbia stocks of sockeye salmon tend to enter fresh water before peak summer temperatures and hold in spawning tributaries for 1 month or more before fall spawning whereas coastal stocks migrate after peak temperatures just prior to spawning (Gilhousen 1990; Hodgson and Quinn 2002). Quinn and colleagues (Quinn and Adams 1996; Quinn et al. 1997; Hodgson and Quinn 2002) have used dam counts and historical records to examine the relationships between run timing and environmental conditions. They found that sockeye salmon passed Bonneville Dam progressively earlier over the period 1949–1993, concomitant with a progressive increase in the mean temperatures that migrating adults experienced in the lower Columbia River (Quinn and Adams 1996). Patterns of individual mortality during 1997 in relation to run timing and temperature were consistent with selection for earlier run timing within these populations, as hypothesized by Quinn and Adams (1996).

If such selection is real and leads to evolution of earlier run timing, we speculate that the energetic costs of migration will increase in coming decades. Recent regional climate projections predict increasingly early winter snowmelt, longer dry periods during summer, and later onset of fall conditions (Parson et al. 2001). If true, these conditions would lead to continued selection for early run timing in Columbia River sockeye and other spring-run salmonids. The energetic costs of migration will likely increase because fish will either hold without feeding in spawning tributaries for longer periods or experience higher temperatures during migration if populations do not respond to selection as rapidly as conditions change or both. This increase in energetic cost could lead to greater in-river or prespawn mortality, particularly in warm years and for stocks migrating long distances.

Scale dependence in patterns of migration behavior and success

Our primary objective was to characterize migration behavior in the hydrosystem and determine if migration behaviors were related to migration success. The relationships between dam passage time and migration rates and migration success were significant when assessed through the lower Columbia River or for all of the migration history, but the relationship between passage time and migration success was not significant when analyzed at individual dams, with the exception of Bonneville Dam. This incongruity suggests that consistently slow passage through multiple projects was associated with unsuccessful migration, but passage times at individual dams by migrants of both types were variable and not significantly different between successful and unsuccessful migrants. The lack of a significant relationship between passage hazard and migration success probably did not result from a lack of statistical power, given our relatively large samples sizes. The scale dependence observed in the effect of migration behavior on migration success illustrates the importance of using fitness-based measures (e.g., survival to spawning tributaries) of performance and examining migration performance throughout the hydrosystem rather than performance at individual locations. Notably, our estimates only include in-river mortality. Prespawn mortality can be high in sockeye salmon populations and we were unable to assess any effects of migration history on prespawn mortality (Gilhousen 1990; Cooke et al. 2004). Therefore, we may have underestimated the effects of migration history on total adult survival.

In summary, these data suggest the potential for an indirect negative hydrosystem effect on migration success in sockeye salmon through the hydrosystem's influence on water temperature. Currently, the relative importance of hydrosystem alterations (i.e., dams) compared with changes in regional climate and land use in contributing to summer warming of the Columbia River is unknown. Nonetheless, we expect the observed pattern of late season mortality to become increasingly important if climate projections hold (Neitzel et al. 1991; Hamlet and Lettenmaier 1999; Parson et al. 2001). In contrast, we found little evidence for a direct effect of individual dams on adult passage in sockeye salmon.

General patterns in migration behavior

We also used telemetry data to examine general patterns of migration behavior throughout the hydrosystem, focusing on patterns of straying, migration over dams, and migration through reaches between dams. Accurate estimates of straying are important for effective management of salmon. In particular, straying and spawning in nonnatal tributaries can affect escapement estimates (Dauble and Mueller 2000). Straying behavior by salmonids occurs naturally and is important for populations because it leads to colonization of new habitats (Milner and Bailey 1989) and avoidance of unfavorable conditions (Leider 1989) and increases genetic diversity (Utter 1991). Sockeye salmon are noted for homing with high precision to their natal streams (Foerster 1936, 1968). In our study, 1.7% (10 of 574) of the radio-tagged sockeye salmon strayed to nonspawning tributaries, similar to the 1.0% stray rate reported by Quinn et al. (1987) for southern British Columbia rivers. Hence, survival estimates from dam counts may be less biased for sockeye than for other salmon species that stray at higher rates (Boggs et al. 2004). Alternatively, the fish that that we considered strays may have been searching rather than straying in the true sense (Griffith et al. 1999). Burger et al. (1995) found that 16% of radio-tagged sockeye salmon temporarily entered a different tributary than the one where they eventually spawned. However, undetected temporary straying was unlikely in the lower Columbia, where 9 out of 10 strays were last recorded, given the extent of telemetry coverage.

Most radio-tagged sockeye salmon passed Columbia River dams rapidly, <24 h after passing tailrace receivers. Median passage time between Rock Island and Rocky Reach dams in our study was 20.7 h compared with a modal time of 53 h reported by Major and Mighell (1967). At each dam, however, 0.2%–8% took more than 5 days to pass, and all time-to-pass distributions were right-skewed. Sockeye salmon passage times were similar to those for summer chinook salmon (*Oncorhynchus tshawytscha*) (medians 12–26.4 h at lower Columbia dams) whose run timing is similar to that of sockeye. In contrast, Columbia River sockeye salmon passed lower Columbia River dams much more quickly than most radio-tagged spring chinook salmon, which had median times between 16.8 and 67.2 h (30% took more than 5 days to pass in 1997; Keefer et al. 2004*c*). Differences in passage time for spring chinook versus summer chinook and sockeye salmon may be related to river conditions. Most spring chinook salmon migrated when flows were relatively high and river temperatures were cool compared with those encountered by sockeye later in the year. Fish may be able to find routes past dams more easily when flow and spill are low, but these effects appear to be relatively weak given the high variability in passage time.

Light level appeared to have the strongest effect on passage time. Specifically, few fish arriving in the tailrace late in the afternoon ascended before spending a night at the dam, consequently increasing passage times. These observations are consistent with previous observations in sockeye salmon (Quinn and Adams 1996) and steelhead (Robards and Quinn 2002) in the Columbia River. Low visibility may make navigation past the relatively complex barriers presented by dams and fishways too difficult for nighttime passage. High turbidity may have further induced daytime passage of dams by sockeye salmon. Secchi disk depths at Bonneville Dam in 1997 were approximately 50% less than the previous 10-year average during the time when radio-tagged sockeye salmon were passing Bonneville Dam, and this high turbidity was presumably caused by the high discharge conditions. In contrast, Hellawell et al. (1974) found that in clear water, most upstream movement of Atlantic salmon (*Salmo salar*) occurred in darkness, suggesting species differences in light sensitivity, complexity of river passage conditions for Atlantic salmon versus Pacific salmon in dam passageways, or both.

Migration rates through the lower Columbia River reservoirs observed here (57–65 km·day^{-1}) are among the highest daily migration rates reported for sockeye salmon. However, the rates are for single reservoir passage, and the median migration rate from Bonneville to McNary, incorporating dam passage times, for our sample was 33.8 km·day^{-1}, in the middle of the values of 22–49 km·day^{-1} reported by Quinn et al. (1997) based on dam counts for this same reach for the period 1954–1994. Migration rates were faster in the lower Columbia River than in the mid-Columbia River, and fish tagged later in the run migrated more quickly in the mid-Columbia River compared with fish tagged earlier in the run. Increasing migration speed for later arriving fish may be related to elevated metabolic activity as temperatures increased, discharge and turbidity decreased, and increased motivation as runs progressed and spawning time approached (Gard 1973; Hellawell et al. 1974; Gilhousen 1990). However, late-arriving fish migrated at a slower rate than those arriving during the peak of migration, again suggesting a potential effect of stressful temperatures on late migrants. Many sockeye salmon were recorded passing upstream in reservoirs and the lower end of the Hanford Reach (the top of the McNary Reservoir) during darkness; nighttime passage through these less heterogeneous environments may explain in part the rapid migration rates in impounded reaches relative to the unimpounded Hanford Reach.

Sockeye salmon migrated through the unimpounded section of the Columbia River (Hanford Reach) at slower rates than reported for several populations of Fraser River sockeye salmon (Killick 1955) and at about half the rate calculated for Columbia River impoundments. Rates for the Hanford Reach in this study were higher than those of sockeye salmon in the Karluk (Gard 1973) and Copper rivers (Merritt and Roberson 1986) and of chinook salmon in the Kenai River (Bernard et al. 1999) but lower than those of chinook salmon and fall-run steelhead in the Hanford Reach in 1997 (Keefer et al. 2004*b*). Slower passage through the Hanford Reach by sockeye salmon, as compared with Columbia River chinook salmon or steelhead, may be related to smaller body size (Brett 1965; Weihs 1973). In comparison with reservoirs, the higher velocities in the Hanford Reach were probably the major contributor to slower migration rates than were observed in the impounded reaches, and it is probable that energy expenditure in this reach was greater than that in reservoirs, despite lower ground speeds. For instance, Merritt and Roberson (1986) found that increased river level significantly decreased travel rate of sockeye salmon within a given year and between years. Notably, the observed rates through the Hanford Reach may underestimate the long-term average because of the high discharge conditions of 1997.

Current and historical estimates of migration rate

The telemetry data allowed us to calculate time budgets for individual fish during migration. Interestingly, the time spent passing the Hanford Reach was proportional to the total migration distance monitored. By extension, the proportion of time spent passing dams and ascending reservoirs was proportional to the distance traveled, suggesting that rapid passage of reservoirs compensated for slowed migration at dams, resulting in similar overall migration rates in the impounded and unimpounded portions of the hydrosystem.

River conditions encountered by migrating Columbia River salmonids have been dramatically altered and the effect of dams on migration times is unknown because no predam data are available. Salmon in unimpounded rivers frequently encounter migration obstacles, such as falls, rapids, or channel constrictions, and dams may not effectively differ from other obstructions. For example, migration speeds for Fraser River sockeye salmon are lowest through constricted and high-velocity areas (Gilhousen 1990; Hinch et al. 1996; Hinch and Rand 1998) and Atlantic salmon migrations are temporarily blocked at falls in Norway (Jensen et al. 1989).

Predam passage rates in the mainstem Columbia River can be estimated from rates for fish in the unimpounded Hanford Reach assuming that passage conditions in this reach are representative of historical conditions throughout the river. Using the rate for sockeye salmon in the Hanford Reach, we estimate that predam Columbia River passage times from river kilometre 235 (Bonneville Dam) to river kilometre 730 (Rock Island Dam) would have been 17.6 days compared with the 17.3 days that we measured in 1997. Similar results were found for spring and summer chinook salmon by applying rates from the unimpounded Snake and Salmon rivers (Keefer et al. 2004*c*). They estimated that predam Columbia and Snake River passage times from river kilometre 235 (Bonneville Dam) to river kilometre 695 (Lower Granite Dam) would have been slightly longer for spring chinook and slightly shorter for summer chinook salmon without the dams. There are clear limitations to such estimates, but they further suggest that rapid migration through reservoirs by adults may largely compensate for slowed migration at dams.

While we found no evidence for negative effects of the Columbia River hydrosystem on adult sockeye salmon passage, inferences based on these data should be made cautiously for at least two reasons. First, because we were unable to assess reproductive success, we do not know how reproductive success is related to migration behavior in the hydrosystem, and any negative indirect effects of dam passage would have gone undetected (e.g., increased prespawning mortality after entering spawning tributaries in sockeye salmon with relatively long passage times). Second, because data were available for only a single (unusual) year, how migration success varies under different environmental conditions remains unknown. Thus, we caution that pronounced direct effects of dam passage may exist, particularly in low-water, high-temperature years. Clearly, more data are needed, both in the Columbia River and in similar rivers without impoundments such as the Fraser River, before a robust picture of sockeye salmon migration and the influence of dams on adult passage is obtained.

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