

Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality?

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Abstract: The relationships among behavior, environment, and migration success in anadromous fishes are poorly understood. We monitored migration behavior at eight Columbia and Snake river dams for 18 286 adult Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (sea-run *Oncorhynchus mykiss*) over 7 years using radiotelemetry. When statistically controlling for variation in flow, temperature, fisheries take, and other environmental variables, we observed that unsuccessful individuals — those not observed to reach spawning areas — had longer passage times at nearly all dams than fish that eventually reached tributaries. In many cases, times were also longer for unsuccessful adults passing through a multiple-dam reach. Four ecological mechanisms may have contributed to these patterns: (i) environmental factors not accounted for in the analyses; (ii) inefficient responses by some fish to passage conditions at dams that resulted in slowed passage, energetic depletion, and unsuccessful migration; (iii) ongoing selection for traits needed to pass obstructions; and (or) (iv) passage rate was not directly linked to migration success, but rather, both resulted from relatively poor phenotypic condition upon river entry in unsuccessful migrants. Overall, these results illustrate the need for a mechanistic understanding of the factors that influence migration success and the need for fitness-based criteria to assess the effects of dams on anadromous fishes.

Résumé : On connaît mal les relations entre le comportement, l'environnement et le succès de la migration chez les poissons anadromes. Nous avons suivi par télémétrie le comportement migrateur de 18 286 saumons chinook (*Oncorhynchus tshawytscha*) et truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) adultes à huit barrages sur le fleuve Columbia et la rivière Snake sur une période de 7 ans. Une fois que nous avons tenu compte statistiquement des variations de débit, de température, de retraits dus à la pêche et des autres variables du milieu, nous observons que les individus qui échouent leur migration — qui n'ont pas été observés sur les sites de fraye — prennent plus de temps pour traverser presque tous les barrages que les poissons qui éventuellement atteignent les tributaires. Dans plusieurs cas, le temps de passage dans les sections avec plusieurs barrages est aussi plus long pour les adultes qui échouent leur migration. Quatre mécanismes écologiques peuvent contribuer à ces patrons: (i) des facteurs écologiques non considérés dans les analyses, (ii) des réactions inefficaces de certains poissons aux conditions de traversée des barrages qui ont pour résultat de ralentir la traversée, d'épuiser les réserves énergétiques et de faire échouer la migration, (iii) une sélection actuelle des caractéristiques nécessaires pour surmonter les obstacles et (ou) (iv) des taux de passage qui ne sont pas reliés directement au succès de la migration, les deux variables s'expliquant plutôt par une mauvaise condition phénotypique lors de l'entrée dans la rivière chez les poissons qui échouent leur migration. Dans leur ensemble, nos résultats indiquent qu'il est nécessaire d'obtenir une compréhension mécaniste des facteurs qui influencent le succès de la migration, ainsi que des critères basés sur la fitness pour évaluer les effets des barrages sur les poissons anadromes.

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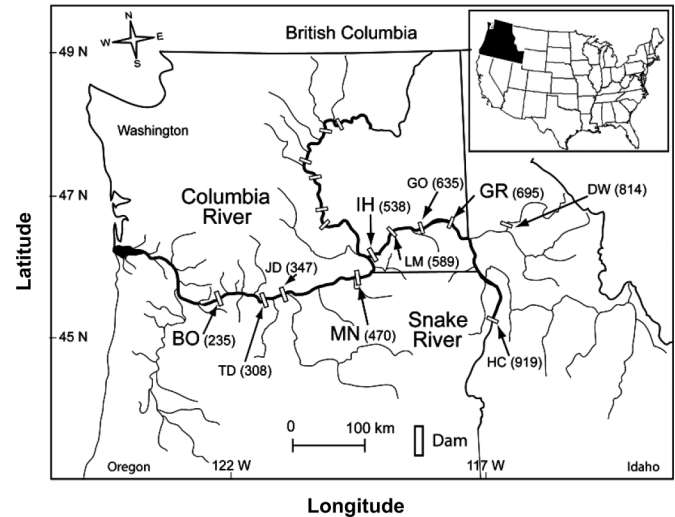
Introduction

The single greatest change to rivers worldwide since the industrial revolution has been the construction of nearly 50 000 dams higher than 15 m (Hart and Poff 2002; Poff and Hart 2002; Postel and Richter 2003). Dams have long been recognized as obstacles to fish migration, and slowed migration or “delay” at dams has been observed in many fish species, including Atlantic salmon (*Salmo salar*) (Karppinen et al. 2002), barbel (*Barbus barbus*) (Lucas and Frear 1997), American shad (*Alosa sapidissima*) (Moser et al. 2000), sea lamprey (*Petromyzon marinus*) (Haro and Kynard 1997), paddlefish (*Polyodon spathula*) (Zigler et al. 2004), and salmonids (*Oncorhynchus* spp.) of the Columbia River Basin (Williams 1998; Keefer et al. 2004a). Dams have frequently been implicated in the decline of resident and anadromous fish populations, in part because of their effects on adult migration (e.g., NRC 1996; Northcote 1998; Dudgeon 2003). Unfortunately, primarily because of logistical constraints, the large body of literature on adult fish passage behavior and performance has been conducted primarily at small scales or at single dams (e.g., Clay 1995; Hinch and Bratty 2000; Bunt et al. 2001), and few studies have examined the relationship between slowed migration and eventual migration success upstream (Naughton et al. 2005).

Similar to many anadromous fishes in regulated rivers, adult Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (sea-run *Oncorhynchus mykiss*) returning to spawning tributaries of the Columbia and Snake rivers must ascend multiple dams (up to nine; Fig. 1). Construction of the Columbia–Snake hydrosystem has been identified as one of several factors causing the decline and listing of more than a dozen salmon and steelhead evolutionary significant units (species, subspecies, geographic races, or populations considered as separate entities for conservation) under the US Endangered Species Act (NRC 1996; Ruckelshaus et al. 2002). Adult fish passage facilities at Columbia and Snake river dams were explicitly designed for the passage of salmonids, and their basic design has been continually refined to enhance their ability to attract and pass both salmonids and nonsalmonid fishes (Monk et al. 1989; Bell 1991; Moser et al. 2002a).

Despite the presence of fish passage facilities and efforts to improve migration conditions at dams, concern remains that slowed migration may have direct or indirect negative effects on adult salmon migration and reproductive success. In the Columbia–Snake system, most adult salmonids pass each dam within 2 days of entering the tailrace and eventually reach spawning tributaries (Keefer et al. 2004a, 2005). However, 1.4%–13.7% of individuals in each run have taken more than 5 days to pass single dams, and some fish take several weeks to pass (Keefer et al. 2004a). Adult salmonids rely on energy reserves gained in the marine environment for migration, suggesting the potential for relatively slow passage to incur a fitness cost. For instance, Geist et al. (2000) estimated that migrating fall Chinook salmon in the Columbia River requiring more than 5 days to pass each dam may have insufficient energy reserves to complete spawning. Whether migratory delay at dams contributes to reduced fitness in anadromous fishes in general or hinders the recovery of Columbia Basin salmonids in particular has been a linger-

Fig. 1. Map of the study region, including location of dams. Fish were collected and tagged at Bonneville Dam. Upstream migration to spawning sites was monitored as far upstream as river kilometre (rkm) 1300 in the Snake River basin or Wells Dam on the Columbia River using 150–170 fixed site antennas and mobile tracking in boats and trucks. Distances from the Columbia River mouth are given parenthetically as rkm. Abbreviations for Lower Columbia River dams: BO, Bonneville; JD, John Day; TD, The Dalles; MN, McNary. Abbreviations for Snake River dams: IH, Ice Harbor; LM, Lower Monumental; GO, Little Goose; GR, Lower Granite; HC, Hells Canyon (impassible); DW, Dworkshak Dam (Clearwater River).



ing question since the construction of dams with fishways. Determining how migration behavior at dams (as measured by passage time) relates to upstream fate is important to understanding how widespread delayed or carry-over effects may be in the ecology of adult anadromous fishes.

During seven migration seasons from 1996 to 2003, we radio-tagged 18 286 returning adult salmonids in four runs (defined by adult return date as spring, summer, and fall Chinook salmon, and summer steelhead). Each run was composed of one or more evolutionary significant units. The general aim of the research has been to identify passage problems and potential solutions. Previously, we have presented general patterns of survival and migration through the hydrosystem (Keefer et al. 2005; Goniea et al. 2006; High et al. 2006) and migration behavior at individual dams and hydrosystem segments (Keefer et al. 2004a, 2004b; Naughton et al. 2005), in tributaries (Keefer et al. 2004c), and in relation to specific passage issues (e.g., Reischel and Bjornn 2003; Boggs et al. 2004; Johnson et al. 2005).

In this study, we tested for an association between fish passage time and eventual fate at two scales: passage at individual dams in the lower Columbia and Snake rivers and total passage time past four dams and through three reservoirs in the lower Columbia hydrosystem. At the first scale, we used Cox proportional hazards regression (PHReg; Allison 1995; Hosmer and Lemeshow 1999) to analyze passage time at each dam in relation to eventual fate while statistically accounting for variation in river environment and fish traits in-somuch as possible. PHReg is particularly well suited to the analysis of passage time data (Castro-Santos and Haro

2003), because the method readily handles cases with incomplete records by censoring and incorporates time-varying covariates — predictor variables whose values are allowed to vary during individual passage events (i.e., river discharge or light level). At the second scale, we used linear models to test whether mean passage times differed between successful and unsuccessful migrants ascending a reach of the lower Columbia River hydrosystem that included four dams and three reservoirs. Overall, the analyses revealed consistent associations between relatively long passage times and eventually unsuccessful migration at both scales. We used results from these two analyses to identify potential underlying mechanisms affecting migration success in anadromous fishes.

Materials and methods

Study system

The Columbia River is the third-largest river system in North America, draining an area of 671 000 km², including nearly all of Idaho and large areas of Oregon, Washington, Montana, and British Columbia (Fig. 1). Mean annual discharge at the river's mouth is approximately 6650 m³·s⁻¹. Fish returning to Snake River drainages must pass the four lower Columbia River dams and most also pass the four lower Snake River dams (Fig. 1). Those returning to Columbia River sites upstream from the Snake River confluence pass a total of four to nine dams. As fish migrate upstream, they encounter 1–2 km long tailraces below dams with turbulent flow caused by discharge from dam turbines and spillways. Fish must distinguish relatively low volume attraction flows leading to fishway entrances at dam faces from the large discharge of turbines and spillways. Once in collection channels, fish pass through transition pools and into ladders, which may be up to 1300 m long, gain 35 m in elevation, and contain 75 or more weirs and pools (Williams 1998).

Most spring and summer Chinook salmon returning to the Snake River basin and lower Columbia River tributaries are stream type Chinook, spending their first year rearing in freshwater before migrating seaward in the spring and summer of their second year. Most adults return after three winters at sea, with some returning after two and four winters (jacks, or precocious males returning after one winter, were not included in this study). Adult fall Chinook salmon return in late summer and early fall, and most spawn in the mainstem Columbia and Snake rivers, especially the 70 km Hanford Reach below Priest Rapids Dam, the only remaining free-flowing stretch of the Columbia River accessible to anadromous fishes upstream from Bonneville Dam. Fall Chinook are ocean type Chinook salmon, as are some summer-run Chinook salmon, migrating to sea in their first year (age 0), returning after two to five winters at sea at age three to six. Steelhead adults may return in any month, though the majority of interior Columbia Basin steelhead enter fresh water in summer and fall and spawn the following spring. Juvenile steelhead reside in fresh water for at least 2 years before outmigrating in spring. Adult steelhead typically return to spawn after one to two winters at sea, and a small proportion (<10%) are iteroparous.

Radio-tagging, telemetry monitoring, and fate assignment

The methods used to radio-tag and monitor salmonid migration and assign fates to individual fish in the Columbia and Snake river basins have been described in detail in Keefer et al. (2004a, 2005). Briefly, fish were diverted from the Washington Shore fish ladder at Bonneville Dam (river kilometre (rkm) 235) into a facility where they could be selected by species. During fall, we targeted “upriver bright” Chinook salmon, a group generally defined as originating east of the Cascade Range; however, run assignment based on timing may have resulted in the inclusion of some ocean-type summer Chinook salmon and tule fall Chinook salmon returning to lower Columbia River tributaries and hatcheries. Diverted fish were anesthetized, sexed, measured for fork length, and inspected for the presence of fin clips indicating known hatchery origin. All fish were tagged with a gastrically implanted radiotransmitter (Lotek Wireless, Inc., Newmarket, Ontario). Prior to 2000, all fish were released about 9.5 km downstream of Bonneville Dam near Dodson, Oregon, or Skamania, Washington. During 2000–2002, 23.2% of spring Chinook salmon, 23.9% of summer Chinook salmon, 35.1% of fall Chinook salmon, and 27.9% of steelhead were released in the Bonneville forebay to meet other study objectives; the remainder were released at the downstream sites. In all years, secondary tags, including passive integrated transponder tags (PIT tags), were used to estimate rates of transmitter loss, which averaged 2.2%–4.0%, depending on species (Keefer et al. 2004d). Individuals with records indicating lost tags were excluded from all analyses.

Adult migration behavior in the Columbia Basin was monitored using an extensive array of approximately 160 radio receiver sites at dams and in tributaries (detailed in Moser et al. 2002b; Reischel and Bjornn 2003; Naughton et al. 2005). Behavior at dams was monitored using fixed aerial and underwater antennas in tailraces and fishways. Major tributaries were monitored with fixed aerial antennas near tributary mouths and with mobile tracking units attached to trucks and boats. Additional data were collected from voluntary returns of transmitters from fisheries (US\$25–\$100 rewards) and from cooperative returns from hatcheries, weirs, and spawning ground surveys operated by federal, state, and tribal agencies.

We used these data to classify individual fish as having reached potential spawning sites (successful migrants), having unknown fates (unsuccessful migrants) as in Naughton et al. (2005), or as fisheries take in the main stem Columbia or Snake rivers. Successful migrants included salmon with telemetry records in known spawning tributaries, those found as carcasses in spawning ground surveys, or those that returned to their hatchery of origin. Beginning in 2000, we were able to identify straying in a subset of radio-tagged adults that had been PIT-tagged during the juvenile stage (i.e., fish of known origin). Strays were identified as known-origin adults having final records in non-natal spawning tributaries. Straying rates were generally low during 2000–2003 (2.2% spring–summer Chinook salmon, $n = 1588$; 4.2% fall Chinook salmon, $n = 166$; 6.8% steelhead, $n = 1414$; M.L. Keefer, C.A. Peery, J. Firehammer, and M.L. Moser, unpublished data), and in the context of this study, we conserva-

tively considered strays to be successful migrants by presuming these individuals had reached potential spawning tributaries. Unsuccessful migrants were salmon with unknown fates whose final telemetry records were outside spawning sites, usually at or between dams, and presumably represent prespawn mortalities, though this group may have included unreported harvest or fish that went undetected in monitored tributaries. Whether fish captured in fisheries would have successfully migrated remains unknown, and hence these fish were excluded from all analyses. We felt these operational definitions accurately represented the fates of the vast majority of fish for several reasons. The rate of transmitter loss through regurgitation was low (Keefer et al. 2004d). The linear nature of the study system, the large number of antenna sites used, and large mobile tracking efforts provided a high probability of detection, particularly at dams. For instance, Naughton et al. (2005) estimated the probability of an individual passing two dams in the mid-Columbia River undetected at $<1.0 \times 10^{-7}$ based on the minimum number of fixed-site receivers salmon passed at these dams and frequencies of receiver outages. While many fish went undetected at individual antennas, it was improbable that misclassification of fates seriously biased our results overall, because any misclassification should act to minimize observed differences in passage behavior between fate groups, rather than create false differences.

Data analysis

For all analyses, we defined passage time as the time elapsed from the first detection at a tailrace antenna 0.5–2 km downstream from the face of a dam to the last record at a fish ladder exit antenna. We conservatively used times for first ascents only at each dam for those fish that fell back downstream (Boggs et al. 2004) and reascended because of the potential for learning or injury to affect subsequent passage times. Other measures of passage time, such as first approach or first entrance to ladder exit, provided qualitatively similar results (C.C. Caudill, unpublished data).

Passage time at individual dams

We used PHReg (Allison 1995; Hosmer and Lemeshow 1999; Castro-Santos and Haro 2003) to model the relationships among observed passage times at individual dams, fate, and other predictor variables using widely available software (PROC PHREG in SAS v.9, SAS Institute Inc., Cary, North Carolina). PHReg models the probability of an event occurring (dam passage) for an individual within a very small time interval as a passage hazard given (i) that the event had not occurred prior to the beginning of the time interval and (ii) a set of predictor variables such as river discharge level and temperature at the beginning of the time interval. Increasing passage hazard corresponds to more rapid passage and shorter passage times. Passage hazards for different groups are expressed as odds ratios; an odds ratio of 2.0 for successful vs. unsuccessful adults indicates successful adults were twice as likely to pass during a time interval as unsuccessful adults. An odds ratio of 1.0 indicates no dif-

ference in probability. We modeled passage hazard in relation to fish fate and environmental factors (flow, temperature, etc.) and fish traits (length, sex, etc.) known to affect migration behavior. The primary advantages of the PHReg method are that it allows predictor variables to vary through time, the censoring of individuals, and the software is widely available. The inability to estimate mean differences in passage time represents the primary disadvantage of the PHReg approach. Other parametric approaches to the analysis of time-event data are available, but do not allow time-varying covariates, require assumptions about the form of the survival function (Allison 1995; Castro-Santos and Haro 2003), or allow time-varying covariates, but currently do not incorporate tests among groups (Moser et al. 2005).

Prior to analysis, we identified a set of 15 candidate models, each consisting of 2–14 predictor variables describing variation in passage environment, fish traits, and individual fate (Table 1; Supplemental Appendix S1³). River environment was described by daily mean values of total discharge (flow), spill (the amount of water passing over the spillway of dams rather than passing through turbines), and temperature because of the potential effect of these factors on salmon behavior and physiology. River environmental data were obtained from Columbia River DART (2005). Few salmon pass ladders at night (e.g., Naughton et al. 2005), and we included a variable coding day vs. night, adjusted for seasonal changes in day length, to account for diel changes in passage behavior. During some periods with low fish passage density (early spring, late fall, and winter), data from Bonneville and McNary dams and Ice Harbor and Lower Granite dams were used to estimate river values at other Columbia and Snake river dams, respectively, because values among dams were highly correlated (e.g., temperature at Bonneville and McNary dams, 1996–2003: $R^2 = 0.98$). We tested for the potential of high fish densities in ladders to slow passage by including the daily dam count of all salmonids and American shad for each dam as separate variables (DART 2005). The above model covariates were time-varying for each fish; those described below were fixed.

The final fate of the fish was the primary predictor of interest. The Cox proportional hazards model assumes the odds ratio between groups remains constant through time. The inclusion of a fate \times passage time interaction both tested for and statistically controlled for deviation from this model assumption (Allison 1995, p. 155). Five additional covariates estimated fish traits: sex, fork length, origin (hatchery or wild), date of tagging as an index of seasonal differences among fish entering the river relatively early or late within each run and (or) unmeasured seasonal trends in environmental variation, and release location (downstream of Bonneville Dam or released to the Bonneville Dam forebay). Interannual differences in river condition have a strong effect on migration behavior (Boggs et al. 2004; Keefer et al. 2004a, 2004b), and consequently, the analyses were stratified by year. The overall effect of year was tested by comparing models with and without year effects, but unfortunately the quantitative differences among years can

³Supplementary data for this article are available on the journal Web site (cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5182. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Table 1. Model-averaged odds ratios and unconditional 95% confidence intervals (CI) from PHReg analyses of passage time at lower Columbia River and Snake River dams.

Dam		Bonneville	The Dalles	John Day	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite
Spring Chinook salmon (<i>Oncorhynchus tshawytscha</i>)									
N	3878	2865	2622	2287	1680	1562	1336	1415	
Censored	145	228	153	217	110	143	23	46	
% Censored	3.7	8.0	5.8	9.5	6.5	9.2	1.7	3.3	
Unsuccessful	644	368	276	151	87	53	30	33	
% Unsuccessful	16.6	12.8	10.5	6.6	5.2	3.4	2.2	2.3	
Estimate									
TOD									
Odds ratio	0.103	0.106	0.066	0.061	0.048	0.066	0.092	0.050	
95% CI	0.089, 0.120	0.089, 0.127	0.052, 0.083	0.047, 0.080	0.034, 0.067	0.048, 0.091	0.068, 0.124	0.035, 0.072	
Flow									
Odds ratio	0.999	0.999	0.998	0.996	0.993	0.997	0.997	1.002	
95% CI	0.996, 1.002	0.997, 1.001	0.996, 1.000	0.993, 0.999	0.989, 0.998	0.993, 1.002	0.993, 1.001	0.994, 1.011	
Temperature									
Odds ratio	1.042	1.135	1.085	1.130	0.989	1.042	1.025	0.942	
95% CI	0.860, 1.262	1.040, 1.238	1.005, 1.170	1.025, 1.245	0.913, 1.070	0.968, 1.123	0.941, 1.117	0.863, 1.029	
Spill									
Odds ratio	0.985	0.983	0.984	0.998	0.968	0.877	0.887	0.847	
95% CI	0.968, 1.003	0.958, 1.008	0.948, 1.022	0.951, 1.047	0.909, 1.030	0.818, 0.941	0.824, 0.955	0.779, 0.920	
Salmon									
Odds ratio	0.968	1.052	1.062	1.048	1.107	1.058	1.000	1.065	
95% CI	0.931, 1.006	1.003, 1.104	1.016, 1.110	1.013, 1.085	1.052, 1.164	1.012, 1.105	1.000, 1.000	1.015, 1.116	
Shad									
Odds ratio	0.178	0.992	0.988	0.974	1.123	1.096	0.999	0.070	
95% CI	0.001, 57.994	0.984, 0.999	0.979, 0.996	0.950, 1.000	1.005, 1.254	0.960, 1.251	0.998, 1.000	0.000, 80.522	
Release site									
Odds ratio	NA	1.436	1.321	1.098	1.068	0.970	1.171	1.236	
95% CI	—	1.233, 1.672	1.127, 1.548	0.926, 1.302	0.892, 1.279	0.798, 1.178	0.962, 1.425	1.008, 1.514	
Fate									
Odds ratio	1.096	1.199	1.292	1.494	1.566	1.461	1.112	2.228	
95% CI	0.953, 1.259	0.993, 1.447	1.048, 1.593	1.154, 1.934	1.107, 2.215	0.911, 2.345	0.538, 2.298	1.053, 4.715	
Fate x Time									
Odds ratio	1.079	1.136	1.089	1.011	1.040	1.294	1.449	1.208	
95% CI	1.044, 1.116	1.070, 1.207	1.040, 1.140	0.951, 1.074	0.961, 1.125	1.012, 1.653	0.873, 2.405	0.902, 1.618	
Sex									
Odds ratio	0.958	0.908	0.980	0.989	1.001	1.026	1.088	0.934	
95% CI	0.889, 1.032	0.828, 0.995	0.894, 1.074	0.893, 1.095	0.891, 1.125	0.903, 1.165	0.957, 1.236	0.825, 1.058	
Tag day									
Odds ratio	1.022	1.012	1.007	1.004	0.998	0.997	1.007	1.007	
95% CI	1.015, 1.029	1.000, 1.024	0.998, 1.016	0.995, 1.013	0.990, 1.006	0.988, 1.007	0.997, 1.017	0.994, 1.020	

Table 1 (continued).

	Dam							
	Bonneville	The Dalles	John Day	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite
Clipped	1.004	1.003	0.936	1.055	0.930	1.096	1.063	0.938
Odds ratio	0.928, 1.087	0.913, 1.102	0.848, 1.033	0.952, 1.169	0.822, 1.053	0.960, 1.251	0.922, 1.225	0.818, 1.076
Length	0.998	0.991	0.989	0.987	1.000	0.989	0.992	0.993
Odds ratio	0.993, 1.003	0.985, 0.998	0.982, 0.996	0.980, 0.994	0.992, 1.009	0.980, 0.999	0.982, 1.002	0.983, 1.003
Summer Chinook salmon								
N	1615	1362	1390	1075	299	283	236	244
Censored	40	49	99	169	8	5	3	5
% Censored	2.5	3.6	7.1	15.7	2.7	1.8	1.3	2.0
Unsuccessful	198	150	121	65	8	5	3	3
% Unsuccessful	12.3	11.0	8.7	6.0	2.7	1.8	1.3	1.2
Estimate								
TOD								
Odds ratio	0.116	0.100	0.162	0.107	0.057	0.008	0.166	0.054
95% CI	0.092, 0.147	0.076, 0.131	0.129, 0.205	0.076, 0.149	0.025, 0.125	0.001, 0.069	0.091, 0.305	0.023, 0.128
Flow								
Odds ratio	1.003	0.997	0.998	1.000	0.999	1.003	1.007	0.985
95% CI	0.998, 1.009	0.995, 1.000	0.996, 1.001	0.994, 1.005	0.980, 1.019	0.990, 1.017	0.985, 1.029	0.967, 1.004
Temperature								
Odds ratio	0.953	0.938	0.972	0.937	1.041	0.979	0.772	0.908
95% CI	0.800, 1.136	0.850, 1.034	0.887, 1.066	0.737, 1.190	0.898, 1.207	0.869, 1.102	0.549, 1.086	0.755, 1.092
Spill								
Odds ratio	0.949	0.978	0.982	0.984	0.898	0.950	0.859	1.185
95% CI	0.915, 0.983	0.934, 1.025	0.937, 1.028	0.926, 1.044	0.755, 1.069	0.805, 1.120	0.705, 1.046	0.867, 1.621
Salmon								
Odds ratio	1.010	1.024	1.052	1.043	2.000	1.320	1.000	2.772
95% CI	0.766, 1.330	0.985, 1.065	1.017, 1.089	0.989, 1.101	1.094, 3.657	0.757, 2.301	0.999, 1.001	1.375, 5.585
Shad								
Odds ratio	0.347	0.997	1.000	1.006	0.993	0.964	1.000	0.977
95% CI	0.064, 1.872	0.994, 0.999	0.997, 1.003	0.993, 1.019	0.951, 1.036	0.909, 1.024	1.000, 1.000	0.441, 2.166
Release site								
Odds ratio	NA	1.776	1.093	1.159	1.468	1.299	1.011	1.492
95% CI	—	1.418, 2.223	0.874, 1.367	0.885, 1.518	0.913, 2.362	0.796, 2.119	0.578, 1.766	0.808, 2.755
Fate								
Odds ratio	0.988	0.946	2.210	1.113	2.402	2.461	8.607	3.211
95% CI	0.759, 1.286	0.685, 1.307	1.571, 3.110	0.622, 1.993	0.575, 10.026	0.458, 13.22	0.387, 191.6	0.053, 195.4
Fate x Time								
Odds ratio	1.304	1.475	1.009	2.054	1.248	0.702	0.536	1.037
95% CI	1.107, 1.535	1.074, 2.027	0.939, 1.085	1.181, 3.572	0.473, 3.293	0.235, 2.091	0.138, 2.075	0.067, 16.100

Table 1 (continued).

	Dam									
	Bonneville	The Dalles	John Day	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite		
Sex										
Odds ratio	0.981	1.076	1.108	1.038	0.790	0.978	1.074	1.142		
95% CI	0.872, 1.103	0.945, 1.225	0.972, 1.264	0.882, 1.220	0.589, 1.059	0.720, 1.329	0.766, 1.506	0.819, 1.592		
Tag day										
Odds ratio	1.012	0.995	1.007	1.017	1.009	0.995	1.051	1.019		
95% CI	0.991, 1.035	0.969, 1.021	0.990, 1.025	1.004, 1.030	0.985, 1.034	0.976, 1.016	0.950, 1.162	0.977, 1.062		
Clipped										
Odds ratio	1.000	1.029	0.968	0.981	0.957	1.168	0.771	0.876		
95% CI	0.884, 1.131	0.895, 1.183	0.839, 1.118	0.829, 1.160	0.709, 1.291	0.858, 1.589	0.532, 1.118	0.620, 1.239		
Length										
Odds ratio	0.987	0.986	0.986	0.985	0.995	0.976	0.984	0.981		
95% CI	0.981, 0.993	0.980, 0.992	0.981, 0.992	0.978, 0.993	0.973, 1.018	0.959, 0.994	0.964, 1.005	0.959, 1.004		
Fall Chinook salmon										
N	2398	1535	1491	1222	231	146	104	63		
Censored	186	145	205	107	42	13	6	6		
% Censored	7.8	9.4	13.7	8.8	18.2	8.9	5.8	9.5		
Unsuccessful	539	248	198	84	25	18	12	9		
% Unsuccessful	22.5	16.2	13.3	6.9	10.8	12.3	11.5	14.3		
Estimate										
TOD										
Odds ratio	0.111	0.088	0.090	0.067	0.081	0.080	0.073	0.170		
95% CI	0.093, 0.133	0.069, 0.111	0.070, 0.115	0.050, 0.089	0.041, 0.161	0.035, 0.185	0.027, 0.198	0.050, 0.577		
Flow										
Odds ratio	0.998	0.995	0.995	0.999	0.984	1.000	1.085	1.060		
95% CI	0.995, 1.001	0.990, 1.000	0.990, 1.000	0.993, 1.004	0.921, 1.051	0.918, 1.090	0.956, 1.232	0.869, 1.295		
Temperature										
Odds ratio	1.076	1.111	1.127	1.045	0.923	0.995	0.951	1.051		
95% CI	1.001, 1.157	0.937, 1.318	0.980, 1.295	0.979, 1.116	0.725, 1.174	0.815, 1.214	0.743, 1.218	0.823, 1.342		
Spill										
Odds ratio	NA	NA	NA	NA	NA	NA	NA	NA		
95% CI	—	—	—	—	—	—	—	—		
Salmon										
Odds ratio	1.009	1.008	1.012	1.005	1.016	1.008	1.000	1.249		
95% CI	0.968, 1.052	0.990, 1.026	0.987, 1.037	0.986, 1.026	0.943, 1.096	0.914, 1.112	1.000, 1.000	1.031, 1.513		
Shad										
Odds ratio	0.000	319.7	0.027	2.775	>10 000	0.000	1.174	0.000		
95% CI	0.000, >10 000	0.022, >10 000	0.000, 265.8	0.011, 717.2	0.000, >10 000	0.000, >10 000	0.903, 1.526	0.000, >10 000		
Release site										
Odds ratio	NA	1.194	1.041	0.990	1.493	0.937	1.764	0.444		
95% CI	—	0.991, 1.439	0.861, 1.258	0.806, 1.216	0.947, 2.354	0.509, 1.722	0.693, 4.491	0.165, 1.193		

Table 1 (continued).

	Dam							
	Bonneville	The Dalles	John Day	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite
Fate								
Odds ratio	1.562	1.511	2.100	2.254	1.385	2.211	0.700	1.175
95% CI	1.280, 1.905	1.242, 1.839	1.491, 2.959	1.552, 3.275	0.653, 2.937	0.847, 5.771	0.175, 2.797	0.152, 9.070
Fate x Time								
Odds ratio	1.043	0.968	1.030	1.036	0.613	1.038	1.286	0.957
95% CI	0.999, 1.089	0.909, 1.031	0.983, 1.079	0.893, 1.202	0.295, 1.276	0.812, 1.326	0.348, 4.757	0.572, 1.603
Sex								
Odds ratio	0.990	1.099	0.995	1.013	1.264	0.985	1.154	0.592
95% CI	0.889, 1.103	0.958, 1.261	0.860, 1.150	0.867, 1.184	0.829, 1.925	0.600, 1.618	0.589, 2.261	0.234, 1.493
Tag day								
Odds ratio	0.995	1.013	1.011	0.996	1.016	0.991	1.031	1.000
95% CI	0.983, 1.006	0.992, 1.034	0.991, 1.032	0.984, 1.007	0.992, 1.042	0.964, 1.019	0.996, 1.067	0.946, 1.058
Clipped								
Odds ratio	1.147	1.007	1.008	0.732	1.261	0.682	0.356	0.282
95% CI	0.958, 1.375	0.790, 1.284	0.772, 1.315	0.561, 0.956	0.764, 2.082	0.348, 1.337	0.108, 1.180	0.047, 1.714
Length								
Odds ratio	0.995	0.993	0.993	0.995	0.976	0.989	0.950	0.978
95% CI	0.989, 1.000	0.986, 1.000	0.985, 1.000	0.987, 1.003	0.954, 0.998	0.962, 1.017	0.914, 0.986	0.933, 1.024
Steelhead (sea-run <i>Oncorhynchus mykiss</i>)								
N	3702	2972	2851	2029	2056	1583	1157	1179
Censored	174	88	246	227	142	48	59	73
% Censored	4.7	3.0	8.6	11.2	6.9	3.0	5.1	6.2
Unsuccessful	932	605	582	339	254	161	90	78
% Unsuccessful	25.2	20.4	20.4	16.7	12.4	10.2	7.8	6.6
Estimate								
TOD								
Odds ratio	0.090	0.126	0.149	0.160	0.124	0.163	0.235	0.089
95% CI	0.077, 0.105	0.110, 0.144	0.131, 0.170	0.138, 0.185	0.106, 0.144	0.140, 0.191	0.201, 0.276	0.071, 0.112
Flow								
Odds ratio	1.001	0.998	0.998	0.997	0.998	0.996	0.998	1.003
95% CI	0.997, 1.006	0.996, 1.000	0.995, 1.001	0.993, 1.000	0.979, 1.016	0.988, 1.003	0.986, 1.009	0.995, 1.012
Temperature								
Odds ratio	0.979	0.962	1.035	1.061	1.066	1.043	1.043	1.049
95% CI	0.936, 1.023	0.935, 0.990	1.011, 1.059	1.021, 1.102	1.027, 1.106	1.023, 1.065	1.015, 1.071	1.022, 1.077
Spill								
Odds ratio	0.974	1.008	0.958	1.007	0.840	0.924	0.836	1.050
95% CI	0.947, 1.001	0.965, 1.054	0.908, 1.011	0.941, 1.077	0.761, 0.927	0.588, 1.451	0.535, 1.306	0.837, 1.317
Salmon								
Odds ratio	1.002	1.014	1.019	1.023	1.046	1.023	1.000	1.082
95% CI	0.935, 1.074	1.005, 1.023	1.002, 1.036	0.987, 1.059	0.957, 1.143	0.979, 1.068	1.000, 1.000	1.002, 1.168

Table 1 (concluded).

	Dam							
	Bonneville	The Dalles	John Day	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite
Shad								
Odds ratio	7.389	1.002	1.005	1.018	1.003	0.972	1.000	0.989
95% CI	0.793, 68.870	0.996, 1.007	0.998, 1.012	0.980, 1.059	0.942, 1.067	0.909, 1.039	1.000, 1.000	0.354, 2.759
Release site								
Odds ratio	NA	1.066	1.122	1.017	1.034	1.039	0.960	1.141
95% CI	—	0.950, 1.196	0.984, 1.278	0.879, 1.177	0.891, 1.201	0.883, 1.223	0.798, 1.155	0.917, 1.419
Fate								
Odds ratio	1.182	1.073	1.347	1.175	1.405	1.333	1.817	2.226
95% CI	1.070, 1.305	0.952, 1.208	1.188, 1.526	0.949, 1.454	1.131, 1.746	1.016, 1.749	1.350, 2.445	1.543, 3.211
Fate x Time								
Odds ratio	1.049	1.046	1.008	1.005	0.970	1.259	0.996	1.008
95% CI	1.025, 1.074	0.996, 1.099	1.000, 1.015	0.980, 1.030	0.926, 1.015	1.075, 1.474	0.964, 1.029	0.968, 1.049
Sex								
Odds ratio	1.052	1.107	1.057	1.024	1.051	1.026	1.079	1.053
95% CI	0.975, 1.136	1.014, 1.207	0.967, 1.155	0.913, 1.149	0.945, 1.170	0.912, 1.153	0.936, 1.244	0.915, 1.213
Tag day								
Odds ratio	1.006	1.004	1.001	1.008	1.006	1.003	1.004	1.004
95% CI	1.003, 1.009	1.001, 1.007	0.998, 1.004	1.002, 1.013	1.001, 1.010	0.997, 1.008	0.998, 1.009	0.996, 1.011
Clipped								
Odds ratio	1.035	1.017	1.006	1.032	0.985	1.020	1.045	0.929
95% CI	0.942, 1.139	0.916, 1.128	0.909, 1.114	0.900, 1.183	0.863, 1.124	0.886, 1.173	0.891, 1.226	0.784, 1.100
Length								
Odds ratio	1.002	0.997	1.012	0.998	1.002	1.006	1.003	1.003
95% CI	0.996, 1.009	0.990, 1.005	1.006, 1.018	0.989, 1.006	0.995, 1.009	0.998, 1.015	0.994, 1.012	0.994, 1.013

Notes: Odds ratios confidence intervals that do not include 1.0 are given in bold. Odds ratios estimate passage hazard (the probability of passage during any given time interval) for one group compared with another. Ratios are expressed as successful:unsuccessful, night:day, downstream:forebay, male:female, hatchery:wild. For example, odds ratios >1.0 for fate indicator a higher passage hazard (and lower passage time) for successful versus unsuccessful adults. Odds ratios for continuous predictor variables estimate change in hazard per unit increase in the predictor. Flow and spill are expressed as change in odds per 283 m³·s⁻¹ (10 000 cubic feet per second), temperature as change in odds per °C, salmonids and shad as change per 10 000 fish in daily ladder count. TOD, time of day (night vs. day); shad, daily dam count of American shad (*Alosa sapidissima*); salmon, daily dam counts of all salmonids (*Oncorhynchus* spp.); NA, not applicable.

not be directly estimated using PROC PRHEG (Allison 1995, p. 160). This analytical limitation also prevented tests of year \times fate interactions.

We used information-theoretic techniques (Burnham and Anderson 2002) to compare among the 15 potential models for each species–dam combination. Akaike's information criterion (AIC) and AIC weights (w_i) were used to identify the most parsimonious model(s), given the data. Model-averaging techniques were used to calculate model-averaged odds ratios and associated unconditional confidence intervals (CIs) that incorporate uncertainty about which model is best (Burnham and Anderson 2002). Details and results of model selection and averaging are given in Appendix S1³. We considered predictor variables to have explanatory power when the 95% CI of the odds ratio did not include 1.0.

On average, 6.7% (range: 1.3%–18.2%) of passage events had uncertain endpoints because of missing telemetry records at the fish ladder exit antenna. These passage events were censored from the analysis by removing them from the risk set at the time of last observation. Operational reasons for incomplete records included antenna outages or passage through an unmonitored navigational lock. Alternatively, individuals were censored because they entered a tailrace but did not pass the dam. We assigned censoring times using the last available record from antennas at the dam, and these were often at antennas near the ladder exit. We tested the effect of this criterion using the sensitivity analyses described below.

A critical assumption of time-event models is that censoring must not be informative with respect to treatment groups (Allison 1995; Hosmer and Lemeshow 1999). We observed that fish with unknown fates were more likely to be censored, violating this assumption (see Results). While the effect of informative censoring on model coefficients cannot be calculated (Allison 1995), the general effect can be assessed by performing sensitivity analyses where censoring times are assigned using different criteria and comparing the resulting estimated regression coefficients with those of the base model. If the coefficients do not change markedly, the effect of this violation on model conclusions is deemed small (Allison 1995). We used three alternative criteria in our analyses. First, we assumed that all censored fish would have passed immediately after the censoring time by including these fish as uncensored and using the censoring time as the time of ladder exit. Second, we assumed that all censored fish could have remained in the risk set until the end of observation by assigning censor times equal to the longest observed passage time. In a third analysis, we excluded a priori all fish that we did not observe to pass the dam under analysis to directly test for any delayed upstream effects of slow passage on fate among those fish that were known to have passed each dam.

Total passage time in the lower Columbia River hydrosystem

We were also interested in the relationship between migration performance and passage time past multiple dams. Specifically, we asked whether fish migration times through the lower Columbia River were longer for unsuccessful than for successful migrants, as observed in sockeye salmon (*Oncorhynchus nerka*) by Naughton et al. (2005). We used

the analysis of variance (ANOVA) model $\log_e(\text{migration time}) = \text{year} + \text{fate} + \text{year} \times \text{fate} + \text{error}$ to test for differences in mean passage time by fate and year. Migration times for each fish were calculated between the first detection in the Bonneville tailrace to exit from a McNary fish ladder (four dams and three reservoirs). By definition, this analysis excluded forebay-released fish and any fish without a ladder exit record at McNary Dam. Passage times were \log_e -transformed to improve the normality of error terms. We also calculated the relative mean difference in passage time between fate classes for each year as $(\text{Time}_{\text{unsuccessful}} - \text{Time}_{\text{successful}}) / \text{Time}_{\text{successful}}$ and then tested whether the mean difference among years differed significantly between fate classes using one-way ANOVA. All statistical analyses were performed in SAS v.9 PROC PHREG or GLM (SAS Institute Inc., Cary, North Carolina).

Results

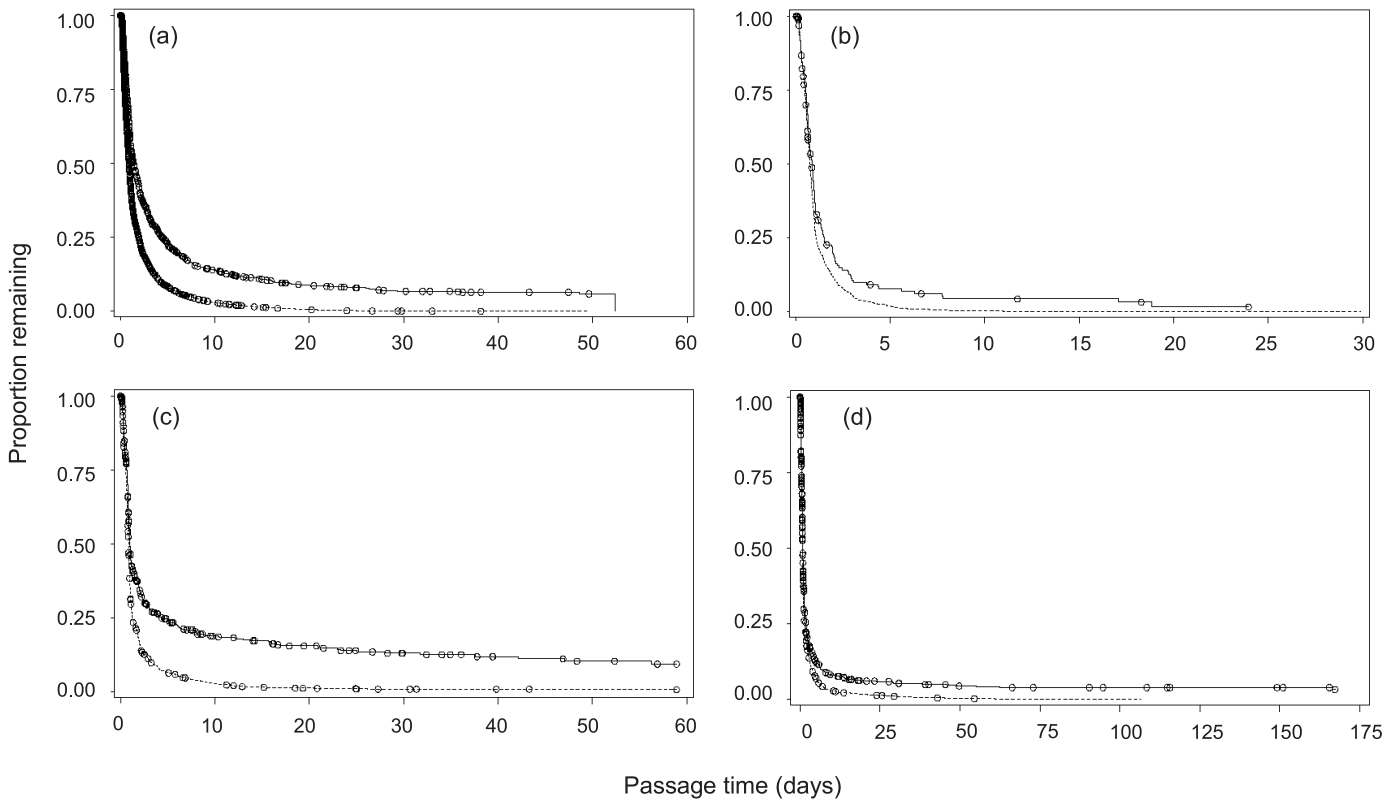
Passage at individual dams

Most individual fish passed each dam rapidly, and median passage times at individual dams ranged from 0.2 to 2.7 days, depending on the species and year (Fig. 2). However, up to 57% of spring Chinook salmon took more than 2 days and as many as 32% took more than 5 days to pass individual dams each year. Summer and fall Chinook salmon passed more quickly than spring Chinook salmon, a pattern thought to be related to temperature effects on swimming speed (Brett 1995) and seasonal differences in discharge (Keefer et al. 2004a). Most steelhead passed during low-discharge conditions and also rapidly passed individual dams.

The results of PHReg multimodel selection using AIC revealed that the full model provided the best fit to the data in the majority of species–dam combinations, though in several cases there was considerable uncertainty about which model provided the best fit to the data (e.g., all model $w_i < 0.4$, Supplemental Appendix S1³). Nonetheless, model coefficients remained nearly identical among models (Supplemental Appendix S1³). There were important differences among years in passage behavior that appeared to be primarily related to annual variation in mean river flow. Though we were unable to directly assess the effects of interannual variation on passage hazard, models not stratified by year had the worst AIC score in all cases (Supplemental Appendix S1³).

Several environmental predictors provided explanatory power for one or more runs within year. Odds ratios compared the probability of passage between categories within any given time interval, or the change in odds as predictor variables increased by one unit. Time of day was the strongest and most consistent effect within year across all runs and dams because few fish passed at night. Individual fish were one-fifth to less than one-twentieth as likely to pass during night as day (Table 1). When different from even, odds ratios for flow were always less than 1.0 and indicated a 0.2%–0.67% decrease in the instantaneous probability of passage per $283 \text{ m}^3 \cdot \text{s}^{-1}$ (10 000 cubic feet per second) increase of flow. Spill had a similar, but stronger effect, with passage hazard decreasing 5.1%–22.1% per $283 \text{ m}^3 \cdot \text{s}^{-1}$. Increasing temperature was generally associated with faster

Fig. 2. Inverse cumulative passage time curves for each run analyzed by fate, all years and dams combined: (a) spring Chinook salmon (*Oncorhynchus tshawytscha*), (b) summer Chinook salmon, (c) fall Chinook salmon, and (d) steelhead (sea-run *Oncorhynchus mykiss*). Note differences in time scale. The passage time curves for unsuccessful migrants are depicted with solid lines; successful migrants are shown with broken lines. Censoring times for individual adults are indicated by open circles.



passage, particularly for spring Chinook salmon, which pass prior to the onset of stressful temperature conditions (e.g., ≤ 18 °C; Table 1). Odds ratios for date of tagging indicated that passage hazard increased $0.4\text{--}5.1\% \cdot \text{day}^{-1}$ within year during the run. This pattern is consistent with other findings that individuals migrating late within runs tend to migrate faster, presumably to reach spawning grounds during the appropriate spawning period (e.g., Quinn and Adams 1996; McLean et al. 2004). In some cases, the number of salmonids present in the ladder was positively associated with passage hazard, revealing that higher densities of adult salmonids within ladders did not slow individual passage. Conversely, at the lower Columbia River dams where large numbers of American shad pass, passage hazards were negatively associated with shad numbers for spring Chinook salmon at all dams except Bonneville Dam. Passage hazard frequently decreased with increasing fish size in the Chinook salmon runs and was not consistently related to sex. Fish released downstream from Bonneville Dam passed more rapidly at The Dalles and John Day dams than those released to the Bonneville Dam forebay for most runs. There was no consistent association between fish origin (hatchery vs. wild) and passage hazard.

The time-event analyses were primarily structured to test for an association between passage time and eventual migration to spawning sites, while statistically controlling for the effects of environmental variables and fish traits. Fate was associated with passage hazard or there was a significant in-

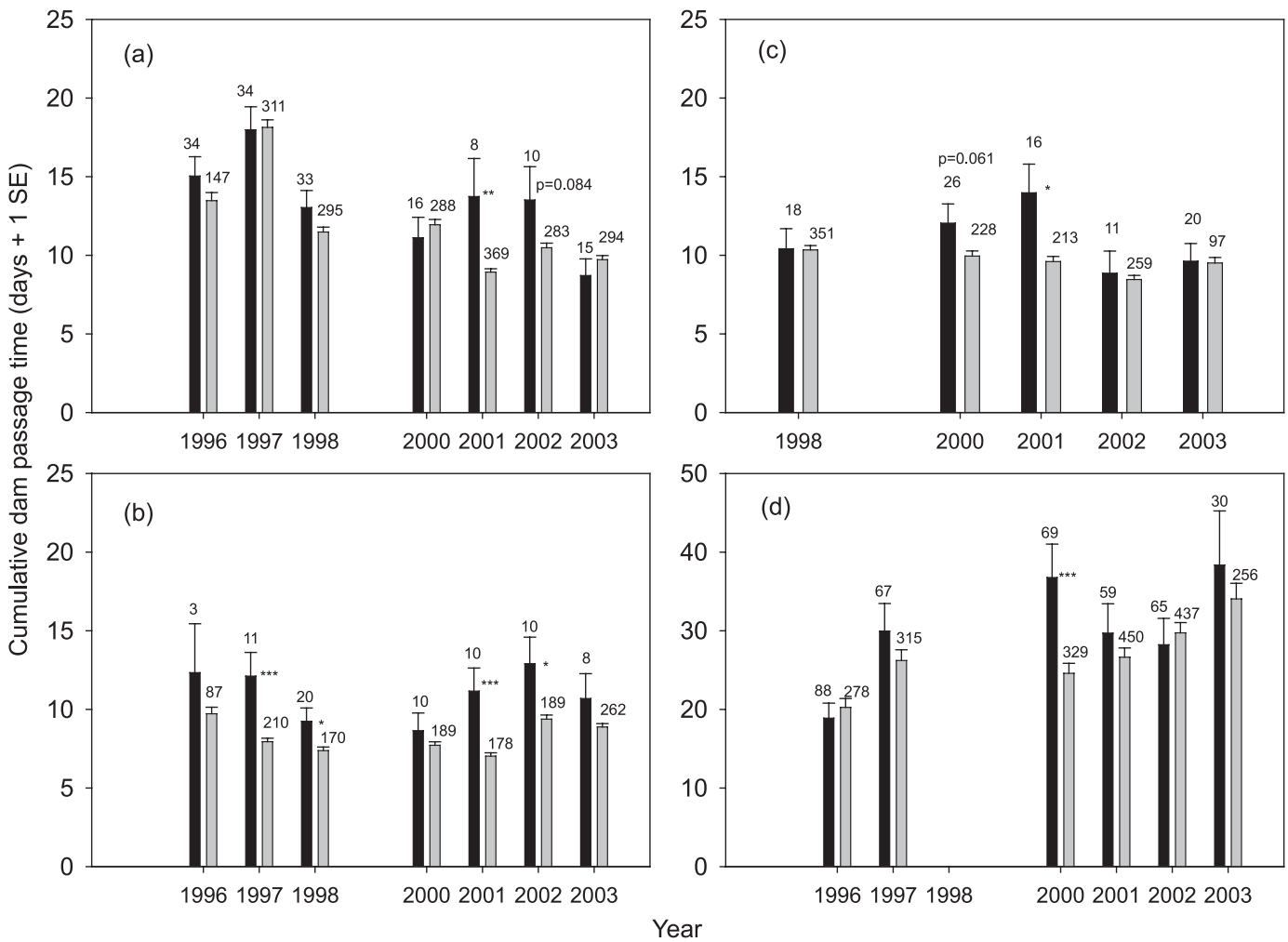
teraction between fate and passage hazard for 22 out of 24 (91.7%) of dam and run combinations, excluding summer and fall Chinook salmon at Snake River dams, where sample sizes were small ($N_{\text{unsuccessful}} < 25$; Table 1). The odds ratio for fate ranged from 1.347 to 2.254 in 11 cases where there was no significant interaction between fate and passage time, indicating that eventually successful fish were 34.7%–225.4% more likely than unsuccessful fish to pass during any given time interval. In one-half of the dam–run combinations (12 of 24, excluding the small samples at Snake River dams), there was a significant fate \times passage time interaction. In all cases, odds ratios were greater than 1.0, indicating that successful fish became increasingly more likely to pass during any given interval as the time since tailrace detection increased compared with unsuccessful fish.

Fish that were eventually unsuccessful were censored significantly more frequently than successful fish in all four runs (Supplemental Appendix S2³), violating an assumption of the Cox proportional hazard regression. The results of three sensitivity analyses differing in their handling of censored fish suggested this violation did not seriously bias the PHReg parameters nor provide false evidence of a relationship between passage time and fate (Supplemental Appendix S2³).

Total passage time through the lower Columbia River hydrosystem

Among Chinook salmon, summer Chinook were fastest

Fig. 3. Mean passage time by fate for each species and year: (a) spring Chinook salmon (*Oncorhynchus tshawytscha*), (b) summer Chinook salmon, (c) fall Chinook salmon, and (d) steelhead (sea-run *Oncorhynchus mykiss*). Unsuccessful adults are indicated by solid bars; successful adults are shown by shaded bars. Note the difference in the y axis for steelhead; passage times were approximately two times longer than Chinook salmon passage times. Sample sizes given above each bar. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.



and spring Chinook had the slowest passage times through the lower Columbia River hydrosystem. In contrast with passage times at individual dams, steelhead passage times through the lower Columbia River hydrosystem were approximately double those for Chinook salmon (Fig. 3), reflecting extended temporary straying by steelhead into cooler tributaries during the warmest months (see Keefer et al. 2004a and High et al. 2006 for more details).

Averaged across all years, mean passage times from the Bonneville tailrace to the McNary Dam forebay (235 rkm and four dams) were faster for successful migrants than for unsuccessful migrants that passed McNary Dam but did not reach spawning tributaries (spring Chinook salmon: $F_{[13,2125]} = 41.73$, $P_{fate} = 0.0190$, $P_{year} < 0.0001$, $P_{fate \times year} = 0.0655$; summer Chinook salmon: $F_{[13,1348]} = 10.42$, $P_{fate} < 0.0001$, $P_{year} 0.0015$, $P_{fate \times year} = 0.4059$; fall Chinook salmon: $F_{[9,1329]} = 4.64$, $P_{fate} = 0.0231$, $P_{year} 0.0198$, $P_{fate \times year} = 0.1657$; steelhead: $F_{[11,2433]} = 7.43$, $P_{fate} = 0.0451$, $P_{year} < 0.0001$, $P_{fate \times year} = 0.0645$; Fig. 3). The observed point estimates for differences between fate groups varied from year to year in all runs except summer Chinook salmon,

with some weak evidence of a fate \times year interaction in spring Chinook salmon and steelhead ($P \leq 0.0655$). The mean annual relative difference in lower Columbia River passage time between fate categories was also significant for all four runs, with unsuccessful passage times 4.2%–16.1% longer than those for eventually successful migrants ($0.0001 < P \leq 0.0451$; Supplemental Appendix S3³). These estimates may have underestimated the true differences in passage time between fate groups because unsuccessful adults not passing McNary Dam could not be included in the analysis.

Discussion

The migration success of adult Chinook salmon and steelhead was inversely related to passage time through the dams and reservoirs of the Columbia River hydrosystem, according to our detailed analysis of radiotelemetric data. We observed that the majority of adult salmonids rapidly passed as many as eight dams and successfully reached their natal spawning sites. However, many fish required more than 2 days to pass individual dams, some took several weeks to

pass, and some did not pass at all. Adults with unknown fates — those that were not detected at spawning sites after passing one or more dams — had consistently longer passage times at individual dams and through a multidam reach of the lower Columbia River. These patterns are striking, but cannot demonstrate an underlying mechanism(s), nor do the relationships reveal the relative importance of dams versus other factors in reducing the migration success of slow adults. However, the patterns in passage time do suggest several potential mechanisms that may have contributed to the observed relationships.

Passage environment and fish traits

Within season, passage hazards were related to time of day, flow, spill, water temperature, densities of adult fishes in ladders, and fish length. The single strongest predictor was time of day, because salmonids infrequently pass dams at night (Naughton et al. 2005). Slower passage at high flows probably reflected both decreased ground speed of fish swimming through higher velocity water (e.g., Hinch and Rand 1998) and an increase in the searching time required to find fishway entrances in a more turbulent tailrace environment. Water was passed over dam spillways during spring and summer in most years, dramatically increasing turbulence in tailraces and potentially accounting for the stronger association of passage hazard with spill than with flow. Detailed analyses of an experiment that manipulated spill levels in the lower Columbia River during 2000–2003 were consistent with those reported here (Caudill et al. 2006a).

Water temperature has dramatic effects on salmon physiology and behavior (Brett 1995). Cool, early spring temperatures (5–8 °C) compared with near optimal late spring temperatures (~15–17 °C; Brett 1995; Salinger and Anderson 2006) probably explain the positive association between temperature and passage hazard for spring Chinook salmon at lower Columbia River dams. Fall Chinook salmon and steelhead encounter warm, and in some cases stressful, temperatures (18–23 °C; Richter and Kolmes 2005) during August and early September and then cooler temperatures as the run season progresses.

The consistent, negative relationship between body length and passage hazard was somewhat surprising because optimal swimming speed increases with body size (Brett 1995). However, the factors influencing optimum swim speed, migration efficiency, and body size are complex (Hinch and Rand 1998; Crossin et al. 2004a; Hughes 2004). Indeed, interpopulation patterns of body size suggest selection for smaller size in long-distance migrating stocks (reviewed in Quinn 2005), though how this would relate to swim speed measured over smaller scales remains unclear. Clearly, the study of the relationships among temperature, body size, swimming speed, and river environment deserves further study.

Interestingly, passage hazards increased, corresponding to shorter passage times, as the number of concurrently passing adult salmonids increased in some models, particularly for Snake River spring Chinook salmon. This result provides no evidence for negative, density-dependent effects and may have resulted from the fact that the peak run presumably occurs during the period of optimal migration conditions, resulting in large numbers of fish moving quickly compared

with early or late in the run. Conversely, the number of American shad was negatively associated with passage hazard in spring Chinook salmon at three out of four lower Columbia River dams. This result suggests the potential for high densities of American shad to slow the migration of salmonids, but could be related to the fact that shad only begin passing Bonneville Dam after most spring Chinook salmon have passed (DART 2005).

Potential underlying mechanisms affecting the passage time – fate relationship

An important question is whether the passage time – fate relationship was caused by impoundment or whether the pattern was primarily related to the rigors of long-distance migration and would have been observed in the unmodified system. In the transformed Columbia–Snake hydrosystem, rapid passage of low-velocity reservoirs appears to compensate for relative slow passage through high-velocity tailraces and over dams (Keefer et al. 2004a; Naughton et al. 2005). Temperature conditions appear to be elevated in the modified system because of the effects of regional climate warming, changing land- and water-use patterns, and the direct effects of impoundment (Quinn and Adams 1996; Quinn et al. 1997), potentially increasing the metabolic costs of migration. Spill frequently elevates dissolved gas levels above saturation and can cause gas bubble disease at extreme supersaturation levels (Johnson et al. 2005), and high spill levels are associated with slowed passage (Caudill et al. 2006a). In contrast, impoundment may reduce migration costs by reducing peak spring flows and because current fish passage facilities may be less challenging in terms of velocity barriers than the cascades and rapids of the predam migration corridor. Historically, migration up the lower Columbia River included dramatic obstacles, such as Cascade Rapids and the 6 m high Celilo Falls, which are both now inundated. Below, we outline four causal mechanisms that may have contributed to the observed passage time – fate relationship.

First, environmental conditions during migration probably contributed to the passage time – fate relationship. Factors that increase the time spent in dam tailraces and fishways, including high spill and flow levels (Caudill et al. 2006a), fallback behavior (Boggs et al. 2004), temperature (Caudill et al. 2006b; Goniea et al. 2006; High et al. 2006), and hydraulics at the base of ladders (Naughton et al. 2006), may be particularly important to the overall energetics of migration and migration success because passage of these areas is energetically demanding (Brown and Geist 2002; Brown et al. 2006). Generally, impoundment, hydrosystem operations, and natural climate drivers affect the environmental conditions encountered by migrating fishes in regulated rivers in ways that probably influence migration success, including in this study. The analysis of passage time data using the PHReg approach provides powerful, dynamic statistical control of measured environmental variation when comparing fate classes, though we note that additional, unmeasured environmental variation in this study that affected both passage time and fate may have contributed to the observed patterns.

Second, variation in passage behavior among individuals may have contributed to the observed passage time – fate relationship. Individual responses to complex hydraulic, tem-

perature, light, olfactory, and other cues during migration are variable (Standen et al. 2004; Caudill et al. 2006b; Keefer et al. 2006). Hinch and Bratty (2000) observed that some sockeye salmon adults exhibited nonoptimal rapid swimming behaviors in high-flow, turbulent areas at Hell's Gate on the Fraser River. Rapid swimming was also associated with unsuccessful passage. Thus, the long passage times and unsuccessful migration of some adults may have been caused by inefficient responses to the passage conditions encountered at dams. Whether relatively slow passage and unsuccessful migration were caused by the artificial conditions at dams or reflect underlying natural variation in behavior remains unknown.

Third, the relationship may represent selection for physiological and locomotory traits needed to traverse velocity barriers at natural falls and artificial channel constrictions. Passage of such velocity barriers is physiologically demanding (Hinch and Rand 1998; Hinch and Bratty 2000; Standen et al. 2002), slowing the upstream migration of fishes in the Columbia–Snake hydrosystem (Williams 1998; Keefer et al. 2004a) and in other salmonid (Karppinen et al. 2002; Laine et al. 2002) and non-salmonid fishes (e.g., Moser et al. 2002a; Zigler et al. 2004). Such barriers may be impassable depending on species and individual fish traits and condition (Moser et al. 2002b; Haro et al. 2004; Reiser et al. 2006). Under this mechanism, relatively weak swimmers would require greater periods to pass individual dams and also be less likely to successfully pass other velocity barriers upstream, including other dams.

Fourth, the relationship may have resulted from variation among individuals in energetic and (or) physiological condition upon river entry, which is determined largely by growth and development in the ocean. Individual salmon differ considerably in total energy content or density upon river entry both within (Pinson 2005) and among years (Crossin et al. 2004b). Adults in poor initial condition, especially those with relatively low energy content, may travel more slowly through high-gradient reaches and be less likely to complete migration. Young et al. (2006) found that among late-run Fraser River sockeye salmon entering fresh water abnormally early, unsuccessful migrants had lower gross somatic energy, higher plasma lactate (indicating recent anaerobic respiration), and higher levels of reproductive hormones, suggesting that unsuccessful individuals had a smaller initial energetic buffer against stress.

Notably, there is potential for these mechanisms to interact. Relatively slow migration past any project could deplete energy reserves, potentially alter subsequent fish behavior and orientation ability, reduce the ability to ascend ladders and traverse velocity barriers, and thereby increase the potential for further slowed and (or) failed migration at upstream dams. Poor initial condition (Crossin et al. 2004a) and (or) environmental conditions (Rand and Hinch 1998) during migration could further increase the probability of a fish entering this cycle. Ocean conditions prior to river entry were considered relatively good during the study period (e.g., Scheuerell and Williams 2005), suggesting reduced migration success and perhaps higher odds ratios for the passage time – fate relationship following a downturn in ocean conditions.

We were able to assess migration success to spawning tributaries and note that relatively slow migration in the hydrosystem may have reduced reproductive success on spawning grounds as well. Migration experience can influence reproductive success (e.g., Patterson et al. 2004), adults with longer migration times consume a greater proportion of energy reserves to reach spawning tributaries (Pinson 2005), and adults may hold for periods of weeks to months prior to spawning. Consequently, low initial energetic content and energetic depletion during migration have been implicated as a contributing factor for prespaw mortality in tributaries (Gilhousen 1990; Cooke et al. 2004; Pinson 2005), an area of increasing concern given high prespaw mortality rates observed in some sockeye and Chinook salmon populations in recent years (Cooke et al. 2004; Pinson 2005).

These results represent one of the first large-scale examinations of the relationship between migration behavior and fate in an anadromous fish. Anadromous and catadromous fishes are thought to be particularly vulnerable to human-induced environmental change because they must have suitable migration corridors in addition to suitable breeding, growth, and (or) overwintering–holding habitats, and because river systems worldwide have been strongly altered by damming and other human activities (Postel and Richter 2003). Long-distance migrating stocks, such as the interior salmonid stocks studied here, may be at particular risk given the relatively high cost of migration, low reserves upon reaching spawning sites, long prespaw holding periods, and marginal thermal regime encountered during migration by some migrants. Clearly, the successful management of habitats for long-distance migrants, especially diadromous fishes, will require mechanistic knowledge of how initial traits and condition, migration behavior, and environmental conditions interact to determine migration performance and reproductive success. The results also illustrate the importance of assessing the indirect effects of dams, including delayed or carry-over effects, because successful completion of migration was clearly associated with passage times and behaviors at downstream dams. Because of logistical and monetary constraints, the vast majority of studies examining the effects of dams on fishes has been conducted at local scales and has focused on short-term phenomena such as behavior at passage structures (i.e., survival past an individual project). Efforts should be made to increase the use of fitness-based performance measures, rather than behavioral or short-term survival criteria, for setting standards for passage facilities and in-river conditions, because long-term population viability ultimately rests on mean fitness remaining at or above replacement.

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