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Factors affecting adult Pacific lamprey passage rates at hydropower dams: using "time to event" analysis of radiotelemetry data

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Abstract

Adult Pacific lamprey (*Lampetra tridentata* Gairdner) encounter up to nine mainstem hydropower dams during their pre-spawning migration in the Columbia River Basin, USA. Radiotelemetry studies indicate that lamprey passage efficiency (the proportion that pass at each dam) is low relative to that of adult salmonids. In addition, lamprey migration is often delayed for over 5 days as they negotiate fishways designed to facilitate salmonid passage. We applied 'time-to-event' analyses (here, time to passage) to 4 years of lamprey passage data by setting the 'hazard rate' of traditional epidemiological studies equal to passage rate. Lamprey passage rates varied as a function of time, along with time-varying predictor variables (such as water temperature, river flow and spill). We used the Akaike Information Criterion to compare several competing versions of the model (each using a different predictor variable). Thus, we were able to distinguish the relative contribution of various factors to migrational delay. By fitting the model with a log-likelihood function, we incorporated information from individual fish rather than aggregated groups of fish. Consequently, this method is able to derive more information from small data sets than more traditional approaches. Moreover, models of this kind allow examination of multiple functional relationships to better explain patterns of fish behaviour obtained from fish telemetry programs.

Introduction

Pacific lamprey (*Lampetra tridentata* Gairdner) are anadromous and may swim hundreds of kilometers to reach spawning locations in the Columbia and Snake Rivers of northwestern USA (Moser and Close, 2003). Although adult Pacific lamprey are parasitic during the marine phase of their life cycle, they detach from their host prior to undertaking this prespawning migration. Therefore lamprey spawning movements are fueled by endogenous reserves, as in many other anadromous species. A notable difference however, is that Pacific lamprey enter fresh water a year prior to spawning (Beamish, 1980). Consequently, the energetic constraints on lamprey movements may be substantially higher than those on other anadromous fish migrations.

Pacific lamprey exhibit low passage efficiency and are delayed at the hydropower dams they encounter on the lower Columbia River (Fig. 1). Whereas 90% or more of the salmonids (*Oncorhynchus* spp.) approaching these dams pass successfully, on average only about 50% of the lamprey pass each of the three mainstem dams that are farthest downstream on the Columbia River (Moser *et al*., 2002). Moreover, lamprey require a median time of 4–6 days to pass the first dam they encounter (Bonneville Dam, Rkm 235), while adult salmonids typically negotiate the fishways at this dam in less than 1 day.

Migration delay at the lower Columbia River dams may reduce lamprey fitness. Negotiating complex fishways and residing in areas of high current velocity is energetically costly (Mesa *et al*., 2003). Lamprey energy reserves are limited, so added time spent migrating and exposure to higher water temperatures during delays may result in reduced spawning success or even inability to reach spawning areas. Also, delay at the dams may expose lamprey to greater predation risk. For example, key predators such as sturgeon and sea lions aggregate below Bonneville Dam and may target lamprey holding at the base of dam (R. Stansell, personal communication, 2004).

In this study, we investigated the factors affecting migration delay of Pacific lamprey by applying "time-to-event" analysis to adult Pacific lamprey passage times. Radiotelemetry was used to obtain the time each individual lamprey required to pass over each dam. The variability in passage time was then related to such abiotic and biotic variables as water temperature, flow, spill, time of day, lamprey size, and the abundance of other species in the fishways. By computing Akaike's Information Criterion we were then able to compare competing models to identify those variables that contributed most significantly to lamprey delay at each dam.

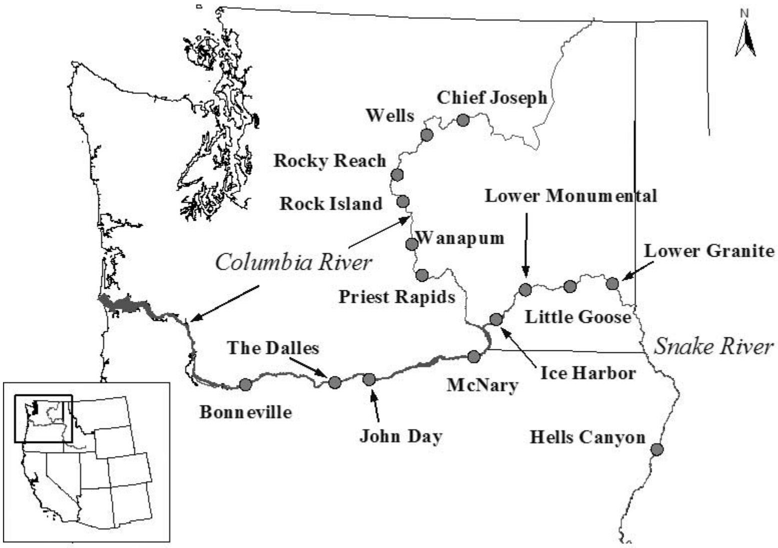

Fig. 1 – The Columbia and Snake River system. Dots indicate the location of mainstem hydropower dams.

Materials and methods

In 1997, 1998, 2000, and 2001, we captured migrating adult Pacific lamprey in a trap deployed nightly at Bonneville Dam (Fig. 1). Fish were anaesthetized (with either 70 ppm tricaine methane sulfonate or 60 ppm clove oil), weighed (to the nearest gram), and measured (to the nearest cm). Using surgical techniques described by Moser *et al*. (2002), a uniquely-coded radio transmitter that represented less than 2% of lamprey body weight was implanted in the body cavity of each fish. The fish were then released 3 km downstream from the dam.

As the lamprey swam back to the base of the dam, they were detected via an extensive array of fixed-site radio receivers (Moser *et al*., 2002). We divided the passage time into two segments. First, the time lamprey spent in the dam tailrace prior to fishway ascension ("tailrace" time) was defined as the time from the first detection at an entrance to a fishway to the time of last entrance into a fishway. Second, the amount of time lamprey required to negotiate the fishway, or "ladder" time, was defined as the time from the last entrance into the fishway to the last detection as the lamprey exited the top of the fishway and moved into the dam forebay. Fish that did not successfully pass over the dam were removed from analysis. Passage times were determined in the same way for lamprey that approached The Dalles Dam (Rkm 308, Fig. 1).

Hourly flow, water temperature, and spill (amount of water released over the dam spillway) were recorded by the US Army Corps of Engineers and these data were downloaded from a website maintained by the University of Washington (DART, 1995). We were also interested in whether crowding by other species in the fishways would affect lamprey passage times. The most abundant fish in the fishways during lamprey migration are American shad (*Alosa sapidissima* Wilson). Daily counts of American shad were taken at each dam and we downloaded these data from DART (1995).

We employed modeling techniques that were initially developed to analyze survivorship in epidemiological studies (Kalbfleisch and Prentice, 1980; Hosmer and Lemeshow, 1999). Researchers have recently generalized these types of analyses from time to death to any "time-to-event" process (Hosmer and Lemeshow, 1999), which in this case was time to passage. Thus, the "survivorship" curve was the proportion of individuals that had not passed as a function of time. The shape of the passage curve is defined by the instantaneous rate of passage, $\lambda(t)$, which can vary through time depending on ambient conditions. In the simplest case, where passage rate is constant with respect to time ($\lambda(t) = \alpha$), the probability that lamprey will remain downstream from a dam as a function of time is an exponential function:

$$\text{Prob(delaying } t \text{ or more days)} = \exp(-\alpha t) \tag{1}$$

where α is the passage rate parameter. With this formulation, an underlying Poisson process describes time to passage, and the mean delay time is $1/\alpha$ (Ross, 1993). Thus as α increases, mean delay time decreases.

We can also express the passage rate as a time-varying function, which is important if individuals face variable conditions during the delay period. In this case, time to passage is described by a nonhomogeneous Poisson process (Ross, 1993), and the delay equation is slightly more complicated:

$$\text{Prob(delaying } t \text{ or more days)} = \exp(-\int_0^t \lambda(\tau)d\tau) \tag{2}$$

This equation integrates over an individual's experience up until time t. Usually the term inside the integral is a simple function and easy to integrate. As an example, we developed a diel model, where passage rate varied according to time of day:

$$\lambda(t) = \begin{cases} \alpha_N \textit{ during night hours} \\ \alpha_D \textit{ during day hours} \end{cases} \tag{3}$$

Based on passage distributions, we defined day as 06:00 to 21:00 and night as the remaining hours.

Next we expanded this model to relate passage rate to predictor variables: lamprey size, flow, spill, water temperature, time of year and shad abundance (in thousands) in the fishways. Since the majority of passage occurs at night, we included only the predictor variables in the night passage rate:

$$\alpha_N(t) = \alpha_0 + \alpha_1 \cdot X_\tau \tag{4}$$

where X_t is a predictor variable (which may be time-varying) and α_0 and α_1 are fitted parameters.

Model parameters were estimated by maximizing the log-likelihood function with respect to the model parameters using the downhill simplex method (Nelder *et al*., 1965; Press *et al*., 1988). The likelihood function is based on the probability density function for delay time t:

$$f(t) = \lambda(t)\exp(-\int_0^t \lambda(\tau)d\tau) \tag{5}$$

The log-likelihood function is then defined as:

$$\log L = \sum_{i=1}^{N} \log f(t_i \mid \alpha) \tag{6}$$

where t_i is the delay time for the ith individual, N is the total number of individuals at a particular dam, and α is the vector of model parameters.

We bootstrapped the data (Efron and Tibshirani, 1986) to obtain approximate 95% confidence intervals (CIs) with the number of bootstrap iterations set at 200. The CIs served to determine the precision of the parameter estimates and to assess whether parameters were significantly different from zero. If the CI for a parameter contained zero, this parameter was not significantly different from zero.

We used Akaike's Information Criterion (AIC) (Akaike, 1973; Burnham and Anderson, 1998) to determine the relative influence of various factors on delay. We considered the diel model to be our null model and determined the importance of various predictor variables by adding spill, flow, water temperature, fish length, shad abundance and time of year to the diel model separately (Equation 4). We quantified the extent of improvement for each alternative model by computing the difference between AIC values for it and the diel model (Δ AIC).

Consequently, the magnitude of the Δ AIC corresponded to the level of improvement in model fit.

Results

The number of lamprey that passed over each dam and were subsequently used in this analysis varied among years and dams (Figs. 2 and 3). The total length of tagged lamprey ranged from 61 to 79 cm (mean=70 cm). The median yearly tailrace time below Bonneville Dam ranged from 0.93 to 3.10 d. At The Dalles Dam, median yearly tailrace time ranged from 0.03 to 1.24 d. After their final entry into the fishway, lamprey also exhibited longer median ladder times at Bonneville Dam (1.09-2.25 d) than at The Dalles Dam (1.01-1.84 d) in each year. In most years, approximately half of the lamprey delayed in the tailrace below the dam for less than an hour before making their final entrance into a fishway (Fig. 2). Fish that did not pass within the first hour sometimes remained below the dam for weeks, and passage patterns for these fish were quite variable across years. In contrast, the passage patterns of lamprey in the ladder were remarkably similar among years within sites, with no statistical difference in passage curves across years at Bonneville (P=0.109, log-rank test) or The Dalles Dams (P=0.306). However, the shape of these curves was significantly different between dams (P<0.001), indicating that lamprey passed through The Dalles Dam fishways faster than through those at Bonneville Dam (Figs. 2 and 3).

Because of the bimodal behavior in delay exhibited by lamprey in the tailrace prior to fishway ascension (Fig. 2), we used only fish that had tailrace times of greater than an hour to model tailrace passage. We used all fish for the analysis of ladder passage since there was no apparent bimodal behavior associated with ladder passage times.

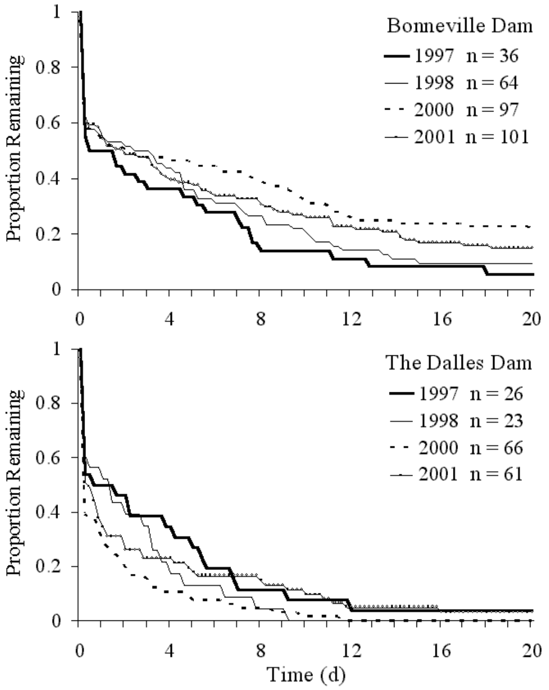

Fig. 2 – The proportion of radio-tagged lamprey that remained in the tailrace below Bonneville (top panel) and The Dalles (bottom panel) dams as a function of time in each year.

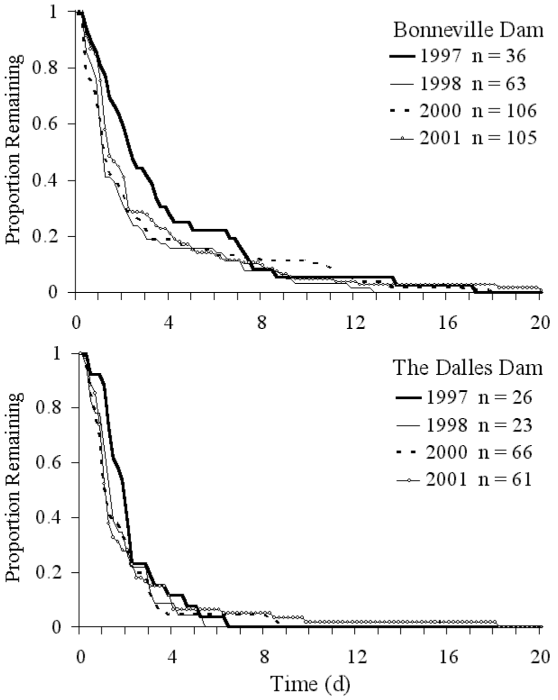

Fig. 3 – The proportion of radio-tagged lamprey that remained in the ladder at Bonneville (top panel) and The Dalles (bottom panel) dams as a function of time in each year.

The diel model (where passage rate varied according to time of day) for both measures of passage time (tailrace and ladder) represented a considerable improvement over the simple model (Tables 1.a-1.d). Passage rates at night (α_N) were significantly higher than daytime rates (α_D) based on the absence of overlap in the 95% confidence intervals for the parameter estimates in nearly every dam and year combination. Due to the obvious nocturnal pattern in lamprey passage rates, we used the diel model as our null model in assessing the effects of other variables.

We determined the improvement in AIC values for each variable and plotted the resulting Δ AIC (Figs. 4 and 5). For both time in the tailrace and the ladders, there were few consistent trends in the effects of a wide range of variables. We assessed the effects of flow and spill on lamprey delay in the tailrace, but not in the ladder because they would not be exposed to these effects in the ladder. Similarly, we only examined the effects of shad abundance in the ladder, as this is where we would expect to see an effect of crowding on lamprey passage rate.

The most consistent effect was that of date. Lamprey that migrated later in the year exhibited less delay in the tailrace than those migrating earlier in the year for 1998 and 2001 at Bonneville Dam and for 1998, 2000, and 2001 at The Dalles Dam (Fig. 4). For the time spent in the ladder, the date model showed substantial improvement in AIC at Bonneville Dam in 2000 and 2001 (Fig. 5). Moreover, at Bonneville Dam in 2000 and 2001, and at The Dalles Dam in 2000, water temperature (which is positively correlated with date) was also negatively correlated with lamprey delay (i.e., lamprey exhibited less delay as water temperature increased, Fig. 5).

There was no indication that lamprey length had any effect on either delay in the tailrace or in the ladders (Figs. 4 and 5). Similarly, spill apparently had no effect on lamprey delay (Fig. 4). Flow was only a significant factor at The Dalles Dam tailrace in 1998. Shad abundance significantly increased lamprey delay in the Bonneville Dam ladders in 2001, and there was no effect of shad on lamprey delay at The Dalles Dam ladders (Fig. 5).

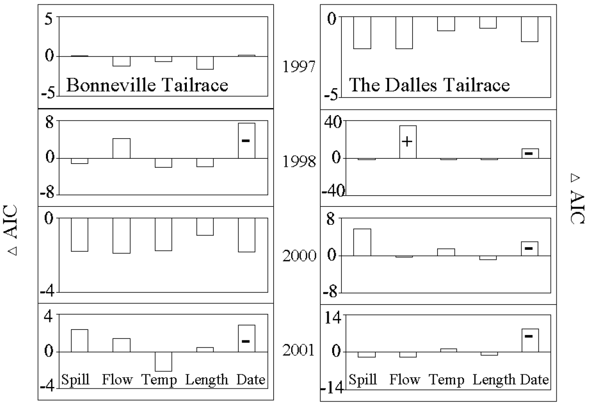

Fig. 4 – The change in AIC (Δ AIC) value with the addition of various factors (spill, flow, water temperature, lamprey length and date) to the null diel model of passage through the tailrace below Bonneville (left panel) and The Dalles (right panel) dams in each year. Symbols in the bars indicate significant effects and the direction of the correlation with delay (i.e., negative relationships indicate that increasing this factor reduces delay).

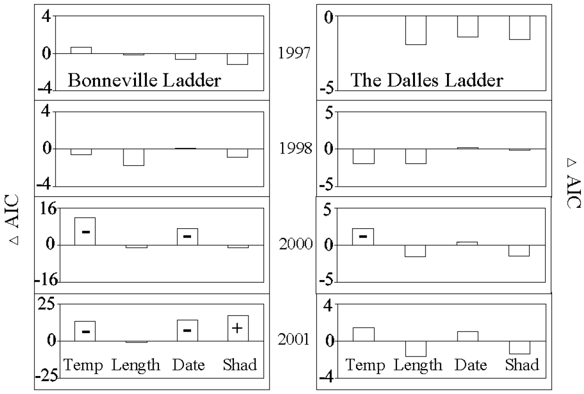

Fig. 5 – The change in AIC (Δ AIC) value with the addition of various factors (water temperature, lamprey length, date and shad abundance) to the null diel model of passage through the ladders at Bonneville (left panel) and The Dalles (right panel) dams in each year. Symbols in the bars indicate significant effects and the direction of the correlation with delay (i.e., negative relationships indicate that increasing this factor reduces delay).

Table 1.a – Parameter estimates (α, α_D, α_N, α_0, or α_1) for tailrace and ladder passage rate models (maximum likelihood estimates). The 95% confidence intervals were obtained by bootstrapping. Higher Δ AIC indicates a better model fit and *n* is the number of fish (Bonneville-Ladder).

Dam/Model	Year	Model	α or αD	C.I.	α0 or αN	C.I.	α1	C.I.	Neg. log likelihood	AIC
Bonneville Ladder	1997 n=36	Simple	0.275	(0.206, 0.398)					82.53	
		Diel	0.136	(0.067, 0.224)	0.497	(0.372, 0.726)			75.41	12.24
		Temperature	0.136	(0.066, 0.229)	-1.271	(-4.241, 1.094)	0.098	(-0.019, 0.306)	74.08	12.88
		Length	0.136	(0.069, 0.243)	-3.131	(-13.824, 2.551)	0.052	(-0.026, 0.257)	74.48	12.09
		Date	0.136	(0.075, 0.232)	-1.060	(-3.522, 3.269)	0.008	(-0.004, 0.024)	74.74	11.57
		Shad	0.136	(0.074, 0.225)	0.560	(0.308, 1.300)	-0.003	(-0.020, 0.007)	74.98	11.08
	1998 n=63	Simple	0.422	(0.322, 0.570)					117.32	
		Diel	0.131	(0.078, 0.208)	0.887	(0.636, 1.343)			93.52	45.60
		Temperature	0.131	(0.075, 0.213)	0.538	(0.109, 1.260)	0.021	(-0.012, 0.346)	92.83	44.99
		Length	0.131	(0.074, 0.221)	2.238	(-2.022, 10.160)	-0.019	(-0.098, 0.047)	93.40	43.85
		Date	0.131	(0.076, 0.218)	-0.907	(-5.896, 2.432)	0.010	(-0.007, 0.042)	92.46	45.73
		Shad	0.131	(0.079, 0.203)	0.926	(0.673, 1.401)	-0.003	(-0.009, 0.005)	92.96	44.72
	2000 n=104	Simple	0.365	(0.283, 0.491)					208.77	
		Diel	0.121	(0.075, 0.196)	0.749	(0.581, 0.995)			172.34	70.85
		Temperature	0.121	(0.074, 0.183)	-2.081	(-3.892, -0.387)	0.148	(0.074, 0.292)	165.44	82.65
		Length	0.121	(0.075, 0.183)	-0.757	(-4.601, 4.384)	0.022	(-0.036, 0.092)	171.95	69.64
		Date	0.121	(0.073, 0.200)	2.457	(0.574, 3.877)	-0.008	(-0.013, 0.003)	167.80	77.94
		Shad	0.121	(0.078, 0.186)	0.755	(0.566, 1.056)	-0.005	(-0.031, 0.012)	171.91	69.73
	2001 n=66	Simple	0.325	(0.255, 0.455)					140.18	
		Diel	0.089	(0.035, 0.171)	0.697	(0.545, 0.988)			112.53	53.30
		Temperature	0.088	(0.040, 0.167)	-3.738	(-6.068, -1.731)	0.246	(0.140, 0.430)	104.90	66.55
		Length	0.089	(0.045, 0.168)	3.124	(-0.508, 7.907)	-0.033	(-0.090, 0.027)	111.87	52.61
		Date	0.089	(0.041, 0.169)	-3.523	(-5.509, -1.292)	0.024	(0.013, 0.040)	104.59	67.17
		Shad	0.089	(0.043, 0.175)	1.013	(0.751, 1.510)	-0.013	(-0.024, -0.007)	102.98	70.40

Table 1.b – Parameter estimates (α, α_D, α_N, α_0, or α_1) for tailrace and ladder passage rate models (maximum likelihood estimates). The 95% confidence intervals were obtained by bootstrapping. Higher Δ AIC indicates a better model fit and *n* is the number of fish (Bonneville-Delay).

Dam/Model	Year	Model	α or αD	C.I.	α0 or αN	C.I.	α1	C.I.	Neg. log likelihood	AIC
Bonneville Delay	1997 n=28	Simple	0.171	(0.111, 0.314)					77.49	
		Diel	0.174	(0.102, 0.329)	0.165	(0.090, 0.338)			77.48	-1.98
		Spill	0.175	(0.076, 0.330)	0.225	(0.047, 0.304)	-0.000	(-0.004, 0.038)	77.42	-1.86
		Flow	0.175	(0.104, 0.357)	0.350	(0.059, 0.488)	-0.001	(-0.012, 0.020)	77.10	-3.22
		Temperature	0.174	(0.085, 0.354)	-0.583	(-3.049, 0.644)	0.042	(-0.014, 0.357)	76.78	-2.57
		Length	0.174	(0.096, 0.417)	-0.401	(-2.057, 4.384)	0.008	(-0.043, 0.056)	77.31	-3.65
		Date	0.175	(0.096, 0.388)	-2.048	(-15.801, 3.537)	0.012	(-0.009, 0.114)	76.38	-1.78
	1998 n=51	Simple	0.144	(0.111, 0.214)					149.67	
		Diel	0.063	(0.036, 0.103)	0.278	(0.200, 0.442)			136.87	23.60
		Spill	0.064	(0.038, 0.101)	0.385	(0.152, 0.409)	-0.001	(-0.005, 0.025)	136.47	22.38
		Flow	0.063	(0.040, 0.132)	0.560	(0.154, 0.595)	-0.001	(-0.008, 0.019)	133.81	27.72
		Temperature	0.064	(0.040, 0.105)	0.281	(0.144, 0.630)	-0.000	(-0.011, 0.012)	136.87	21.60
		Length	0.064	(0.037, 0.104)	-0.057	(-3.170, 1.938)	0.005	(-0.019, 0.053)	136.81	21.70
		Date	0.064	(0.036, 0.103)	-0.837	(-2.107, 0.081)	0.006	(0.002, 0.019)	132.19	30.96
	2000 n=65	Simple	0.064	(0.051, 0.085)					243.80	
		Diel	0.035	(0.022, 0.054)	0.112	(0.085, 0.156)			232.97	19.68
		Spill	0.035	(0.023, 0.055)	0.126	(0.079, 0.224)	-0.000	(-0.001, 0.001)	232.87	17.86
		Flow	0.035	(0.022, 0.059)	0.090	(-0.089, 0.358)	0.000	(-0.001, 0.001)	232.91	17.78
		Temperature	0.035	(0.022, 0.053)	0.028	(-0.329, 0.474)	0.004	(-0.013, 0.025)	232.84	17.93
		Length	0.035	(0.023, 0.059)	-0.227	(-0.898, 0.430)	0.005	(-0.003, 0.016)	232.43	18.75
		Date	0.035	(0.023, 0.053)	0.064	(-0.122, 0.402)	0.000	(-0.001, 0.001)	232.89	17.84
	2001 n=76	Simple	0.099	(0.079, 0.133)					251.58	
		Diel	0.031	(0.018, 0.047)	0.211	(0.152, 0.293)			222.83	55.50
		Spill	0.032	(0.017, 0.048)	0.182	(0.127, 0.273)	0.003	(0.000, 0.010)	220.63	57.89
		Flow	0.032	(0.019, 0.054)	-0.025	(-0.309, 0.277)	0.002	(-0.000, 0.006)	221.12	56.92
		Temperature	0.032	(0.020, 0.053)	0.231	(-0.445, 0.611)	-0.001	(-0.016, 0.039)	222.88	53.40
		Length	0.032	(0.019, 0.053)	1.211	(-0.023, 2.991)	-0.014	(-0.034, 0.005)	221.62	55.92
		Date	0.031	(0.017, 0.052)	-0.302	(-0.721, 0.347)	0.003	(-0.000, 0.006)	220.39	58.38

Table 1.c – Parameter estimates (α, α_D, α_N, α_0, or α_1) for tailrace and ladder passage rate models (maximum likelihood estimates). The 95% confidence intervals were obtained by bootstrapping. Higher Δ AIC indicates a better model fit and *n* is the number of fish (The Dalles-Ladder).

Dam/Model	Year	Model	α or αD	C.I.	α0 or αN	C.I.	α1	C.I.	Neg. log likelihood	AIC
The Dalles Ladder	1997 n=22	Simple	0.891	(0.703, 1.223)					24.53	
		Diel	0.135	(0.052, 0.397)	2.038	(1.528, 2.644)			11.77	23.52
		Temperature	0.134	(0.055, 0.356)	-7.961	(-62.379, -2.659)	0.496	(0.268, 4.495)	10.77	23.52
		Length	0.135	(0.055, 0.410)	-2.202	(-23.530, 17.309)	0.058	(-0.200, 0.409)	11.72	21.61
		Date	0.134	(0.059, 0.444)	-2.870	(-9.395, 1.519)	0.024	(0.006, 0.071)	11.46	22.13
		Shad	0.135	(0.053, 0.471)	2.019	(1.472, 2.583)	-0.053	(-0.478, 0.290)	11.56	21.94
	1998 n=23	Simple	0.622	(0.466, 0.955)					33.92	
		Diel	0.357	(0.160, 0.713)	1.029	(0.720, 1.560)			30.80	4.24
		Temperature	0.368	(0.167, 0.737)	1.023	(-56.117, 1.533)	0.000	(0.000, 3.839)	30.80	2.25
		Length	0.357	(0.138, 0.754)	1.011	(-27.282, 33.700)	0.000	(-0.270, 0.929)	30.80	2.24
		Date	0.357	(0.163, 0.728)	-5.744	(-12.733, 3.158)	0.037	(-0.003, 0.081)	29.68	4.49
		Shad	0.357	(0.159, 0.619)	1.204	(0.713, 2.405)	-0.016	(-0.104, 0.022)	29.88	4.09
	2000 n=66	Simple	0.598	(0.486, 0.795)					99.97	
		Diel	0.203	(0.124, 0.349)	1.256	(0.941, 1.675)			76.48	44.96
		Temperature	0.203	(0.123, 0.316)	-2.499	(-8.261, 1.660)	0.187	(0.001, 0.495)	75.35	47.23
		Length	0.203	(0.123, 0.340)	-1.006	(-5.386, 4.861)	0.033	(-0.038, 0.111)	76.27	43.40
		Date	0.203	(0.112, 0.358)	3.879	(0.212, 9.103)	-0.012	(-0.028, 0.011)	75.28	45.38
		Shad	0.203	(0.117, 0.354	1.226	(0.913, 1.705)	-0.000	(-0.240, 0.375)	76.21	43.51
	2001 n=61	Simple	0.512	(0.395, 0.752)					101.80	
		Diel	0.258	(0.171, 0.460)	0.926	(0.693, 1.353)			90.02	21.57
		Temperature	0.258	(0.144, 0.395)	-1.383	(-4.908, 2.483)	0.116	(-0.058, 0.315)	89.29	23.03
		Length	0.258	(0.140, 0.495)	-0.785	(-6.875, 7.240)	0.024	(-0.063, 0.119)	89.85	19.90
		Date	0.258	(0.161, 0.449)	2.936	(-2.836, 5.271)	-0.009	(-0.018, 0.020)	88.48	22.65
		Shad	0.258	(0.143, 0.444)	0.902	(0.626, 1.395)	0.003	(-0.046, 0.019)	89.69	20.22

Table 1.d – Parameter estimates (α, α_D, α_N, α_0, or α_1) for tailrace and ladder passage rate models (maximum likelihood estimates). The 95% confidence intervals were obtained by bootstrapping. Higher Δ AIC indicates a better model fit and *n* is the number of fish (The Dalles-Delay).

Dam/Model	Year	Model	α or αD	C.I.	α0 or αN	C.I.	α1	C.I.	Neg. log likelihood	AIC
The Dalles Delay	1997 n=18	Simple	0.183	(0.111, 0.413)					48.52	
		Diel	0.081	(0.026, 0.240)	0.355	(0.197, 0.752)			44.03	6.98
		Spill	0.082	(0.024, 0.238)	0.324	(0.114, 0.787)	0.000	(-0.001, 0.077)	44.03	4.98
		Flow	0.081	(0.025, 0.245)	0.372	(0.113, 0.878)	-0.000	(-0.020, 0.052)	44.03	4.98
		Temperature	0.081	(0.028, 0.244)	2.014	(-7.612, 9.581)	-0.086	(-0.390, 0.526)	43.46	6.12
		Length	0.082	(0.018, 0.202)	-1.404	(-11.362, 3.152)	0.026	(-0.028, 0.249)	43.39	6.27
		Date	0.081	(0.021, 0.202)	1.520	(-9.205, 6.360)	-0.006	(-0.023, 0.081)	43.80	5.44
	1998	Simple	0.325	(0.227, 0.553)					33.99	
		Diel	0.098	(0.028, 0.204)	0.704	(0.386, 1.306)			27.56	10.85
		Spill	0.098	(0.031, 0.213)	1.341	(0.181, 5.539)	-0.006	(-0.034, 0.016)	27.09	9.80
		Flow	0.097	(0.034, 0.150)	18.941	(3.128, 42.556)	-0.086	(-0.149, -0.006)	9.04	45.90
		Temperature	0.097	(0.033, 0.202)	0.844	(-11.636, 1.634)	-0.008	(-0.039, 0.871)	27.52	8.93
		Length	0.098	(0.030, 0.210)	2.611	(-7.763, 14.620)	-0.027	(-0.164, 0.144)	27.50	8.98
		Date	0.098	(0.032, 0.196)	-9.955	(-73.188, -5.578)	0.059	(0.035, 0.458)	21.45	21.08
	2000 n=31	Simple	0.367	(0.272, 0.611)					62.10	
		Diel	0.113	(0.040, 0.234)	0.797	(0.552, 1.479)			49.76	22.68
		Spill	0.113	(0.037, 0.220)	1.762	(0.404, 1.521)	-0.020	(-0.010, 0.107)	45.92	28.35
		Flow	0.113	(0.046, 0.221)	1.576	(0.455, 1.962)	-0.006	(-0.040, 0.055)	48.94	22.31
		Temperature	0.113	(0.037, 0.247)	6.119	(0.690, 14.463)	-0.256	(-0.596, 0.003)	48.03	24.15
		Length	0.113	(0.037, 0.244)	3.318	(-2.959, 14.737)	-0.036	(-0.147, 0.064)	49.21	21.77
		Date	0.113	(0.038, 0.233)	-2.319	(-7.498, 0.321)	0.014	(0.004, 0.055)	47.22	25.75
	2001 n=42	Simple	0.203	(0.138, 0.387)					108.99	
		Diel	0.061	(0.027, 0.162)	0.445	(0.252, 1.134)			91.88	32.22
		Spill	0.061	(0.027, 0.138)	0.472	(0.185, 1.927)	-0.002	(-0.007, 0.070)	91.79	30.39
		Flow	0.061	(0.022, 0.153)	0.527	(0.205, 1.481)	-0.001	(-0.031, 0.046)	91.84	30.31
		Temperature	0.061	(0.024, 0.165)	-1.169	(-8.827, 3.202)	0.080	(-0.098, 0.612)	90.32	33.35
		Length	0.061	(0.025, 0.181)	2.326	(-0.772, 8.992)	-0.026	(-0.087, 0.041)	91.34	31.29
		Date	0.061	(0.024, 0.169)	-1.779	(-5.902, -0.060)	0.011	(0.003, 0.047)	86.47	41.03

Discussion

The time-to-event analysis we used to examine lamprey delay offers some decided advantages over more traditional approaches. This method takes into account the temporal variability in environmental predictors that is not distinguished by methods that group passage times into bins. In cases where environmental data are available on fine temporal scales (in this case hourly), time-to-event analyses incorporate this information and increase the precision of correlations. In addition, these analyses require smaller sample sizes because each fish is treated independently and the outcomes are not affected by the non-normal distribution characteristic of passage rates in fish.

Predictive models of this type may be useful for management of hydropower dams to benefit fisheries resources. Our analysis indicated that there were significant differences in passage rates at the two dams we examined. Although we dissected the lamprey passage into two distinct phases (delay in the tailrace and in the ladder), our analysis indicated that there were significant and consistent improvements in both measures at The Dalles Dam relative to Bonneville Dam. Subsequent analysis did not indicate that environmental factors affected by dam operation, such as flow or spill, were important predictors of lamprey delay at either dam. We hypothesize that differences in fishway construction at the two dams affected passage rate, as they do passage efficiency (Moser *et al*., 2002). An alternative hypothesis is that lamprey at The Dalles Dam are more motivated or more able to negotiate the fishways due to the date of passage. In our analysis of a variety of predictor variables, the only consistent improvement to the diel model resulted when we added the effects of date. It is unlikely that this effect was due to the stage of reproductive maturity, as Pacific lamprey in this system do not spawn until the year after river entry. We found that lamprey exhibited decreased delay below the dams as the season progressed. Moreover, they exhibited some decreases in delay with increasing water temperature (which is correlated with date) in the ladders. Consequently, improved passage at The Dalles Dam may be partly attributed to the fact that lamprey passed this dam later in the year.

Recent laboratory measurements of lamprey swimming performance indicated a slight, yet significant decrease in swimming performance of radio-tagged lamprey when compared to controls (Mesa *et al*., 2003). If there was a significant effect of relative tag size on lamprey passage rate, it would have been reflected in an improvement in AIC values when we modeled the effects of lamprey length. Instead, we found that there was a consistent decrease in AIC when we added the length variable, indicating that there was no effect of lamprey size on delay either in the tailrace or in the fishways.

The clear improvement in the diel model over the simple exponential function describing the probability of delay indicated that our analysis is sensitive to patterns of lamprey behavior. While the fact that adult lamprey are primarily nocturnal is well-documented (Steir and Kynard, 1986; Almeida *et al*., 2002), the effects of other abiotic and biotic variables on passage rate have not been described. We found that the date of passage was an important factor affecting lamprey delay, but that other abiotic predictor variables did not have any significant or consistent effect on delay. Almeida *et al*. (2002) noted that adult sea lamprey (*Petromyzon marinus* Linnaeus) migration in the River Mondego, Portugal, was stimulated by increased flow. However, we found no evidence that Pacific lamprey delay was negatively correlated with flow. This may be due to the fact that increased flow at the base of dams is associated with increased turbulence, whereas increased flow in reservoirs, like the River Mondego results in higher velocity, uni-directional currents.

Interestingly, we found that abundance of shad in the fish ladders at Bonneville Dam was positively correlated with lamprey delay in 2001. Of the four study years, 2001 was the year with the highest total shad abundance and the lowest water levels. Consequently, negative effects of shad on lamprey passage rates would be most pronounced in 2001. It is possible that this result is spurious, as no significant effect of shad abundance was found at The Dalles Dam ladders or in any other year. However, this finding suggests that further investigation of biotic interactions in the fish ladders is warranted. We caution that the data used in our analysis represent only a fraction of the adult Pacific lamprey migrating through the lower Columbia River. The fish were initially collected in a fishway at Bonneville Dam, and therefore are not representative of the entire population downstream of the dam. We also eliminated from analysis those fish that did not successfully pass over a dam. Moreover, for the analysis of tailrace delay, we eliminated the lamprey that required less than 1 hour to make a final entrance into a fishway. Consequently, while the sub-sample we used illustrates the use of this technique, it does not necessarily provide a comprehensive analysis of all lamprey behaviours.

The approach we present is a simple comparison of single factor models. The time-to-event analysis allows construction of more complex multifactorial models that may be necessary to distinguish the effects of environmental variables that are correlated (such as time of year and water temperature). In addition, there are a host of other predictor variables that could be tested. For example, we found that delay below the dam was distinctly bi-modal, which may be due to reproductive readiness. A physiological marker of reproductive condition may therefore be a useful predictor of lamprey delay. Nevertheless, the simple methods employed here indicated that time-to-event analysis is useful in describing lamprey passage rates and can be used with relatively low sample sizes. Efforts to reduce lamprey delay at hydropower dams will benefit from an even more comprehensive assessment of factors to allow prediction of lamprey behaviour.

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