A Model Linking Ocean Survival to Smolt Length

Gregor Passolt and **James J. Anderson**

School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020, USA

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The survival of juvenile salmon in their freshwater environment and first year in the ocean depends on their size, such that bigger fish generally survive better. However, studies contradict each other about the importance of this relationship and the form it takes, while others find equivocal or negative results (Sogard 1997). Previous work on Pacific salmon (*Oncorhynchus* spp.) focused on the presence or absence of a length effect on recruitment, but only recently have attempts been made to develop a mathematical form of the relationship (Satterthwaite et al. 2009; Hunsicker et al. 2011). Koenings et al. (1993) used non-parametric Loess smoothing to find common patterns in survival with respect to length, but no general theory has emerged. Although a size-selective survival effect is generally acknowledged and is found in data (Henderson and Cass 1991; Saloniemi et al. 2004), it is sometimes not observed (Rechisky 2010), or the effect is negative, i.e., larger fish having poorer survival (Ewing and Ewing 2002). Understanding the factors that determine size-dependent survival in salmon is important because the ecology of size links closely with recruitment and raises the question of whether large releases of hatchery salmon smolts limits the growth rate of both wild and hatchery fish and thus reduces their survival to adult stages.

As a step in characterizing this linkage, we developed a 4-parameter model relating the survival of juvenile salmonids to their size based on susceptibility to predation. The model is parameterized to test the hypothesis that there is a critical size beyond which smolts experience significantly lower mortality due to a reduction in gape-limited predation. The model was tested with spring-run Chinook salmon (*O. tshawytscha*) tagged in the Columbia River Basin. We apply the model to characterize juvenile survival during river migration and survival from juvenile release to adult return.

Dividing prey mortality into size-dependent and size-independent causes, a differential equation can express the mortality rate experienced by salmon of a certain size as

$$\frac{dN_x}{dt} = -c_1 N_x - c_2 N_x P_x$$

where N_x is the number of smolts of size x, and P_x is the fraction of the total predator population capable of consuming smolts up to size x. The rate of change in number of fish has one part independent of predators (first term) and one part dependent on the number of predators (second term). Parameters c_1 and c_2 are constants assumed to be independent of fish size but may vary from fish stock and by year. The solution of the equation expressing size-specific survival is $S_x = N_x(t)/N_x(0) = c_3 \exp(-c_4 P_x)$ where the size independent mortality is contained in the constant c_3. Using a Taylor expansion of the exponential, $e^{-y} = 1 - y + y^2/2! - + y^3/3! + \ldots$, and truncating at the first power because $c_4 P_x < 1$, then the survival is approximated as $S_x \approx k_0 + k_1(1 - P_x)$ where k_0 is the base survival of the smallest fish and k_1 is the maximum survival improvement such that $k_0 + k_1$ is the survival of fish that are too large for the predators.

We assume predators have a normal size distribution and express their density in terms the size of prey they are able to consume as

$$S_x \approx k_0 + k_1 \Phi\left(\frac{x - x_c}{\sigma}\right)$$

Where Φ is the cumulative distribution of predator size expressed in terms of the smolt size susceptible to 50% of the predators, x_c, and the standard deviation of the distribution is σ.

To test the model, three distinct data sets were used in which out-migrating spring Chinook salmon from the Columbia River basin were tagged with Passive Integrated Transponder (PIT) tags. For freshwater survival, PIT-tagged salmon smolts were released at Sawtooth and Rapid River hatcheries on the Salmon River and detected at Lower Granite Dam or farther downstream (Fig. 1). At Sawtooth Hatchery (747 km upstream of Lower Granite Dam; Fig. 1) in 1998, 7039 smolts were tagged and 15.7% reached the dam. In 1991, 7081 fish were tagged and 6.6% reached the dam. At Rapid River Hatchery (283 km above the dam) the number of fish released over the years 1993-2008 varied and survival to the dam ranged between 6.6 and 54.7% (Table 1).

All correspondence should be addressed to G. Passolt.
e-mail: gregorp@u.washington.edu

Table 1. Summary of spring Chinook salmon tagged at Rapid River Hatchery and survival to Lower Granite Dam.

Year	Number tagged	Survival (%)	Mean length (mm)
1994	2910	35.12	119.2
1995	1961	61.45	120.8
1996	19072	43.73	124.4
1998	48339	59.62	117.5
1999	45409	61.65	120.8
2000	47577	54.69	119.6
2001	54915	67.11	119.0
2002	182913	60.26	122.7
2003	135717	47.43	120.1
2005	5277	70.21	123.9
2006	49871	61.63	122.0
2007	55584	55.33	115.2
2008	70711	65.61	122.8

The survival of fish released as smolts at Lower Granite Dam and then detected as adults at Bonneville Dam one to three years later was determined for years 1998–2009 (Fig. 1). For this third data set, fish were distinguished by hatchery- or wild-origin and whether they passed through the hydrosystem (Lower Granite Dam to Bonneville Dam) as run-of-river migrants or were collected in barges at Lower Granite Dam and released below Bonneville Dam. Numbers tagged and survival from smolt release to adult return (SAR) are given in Table 2.

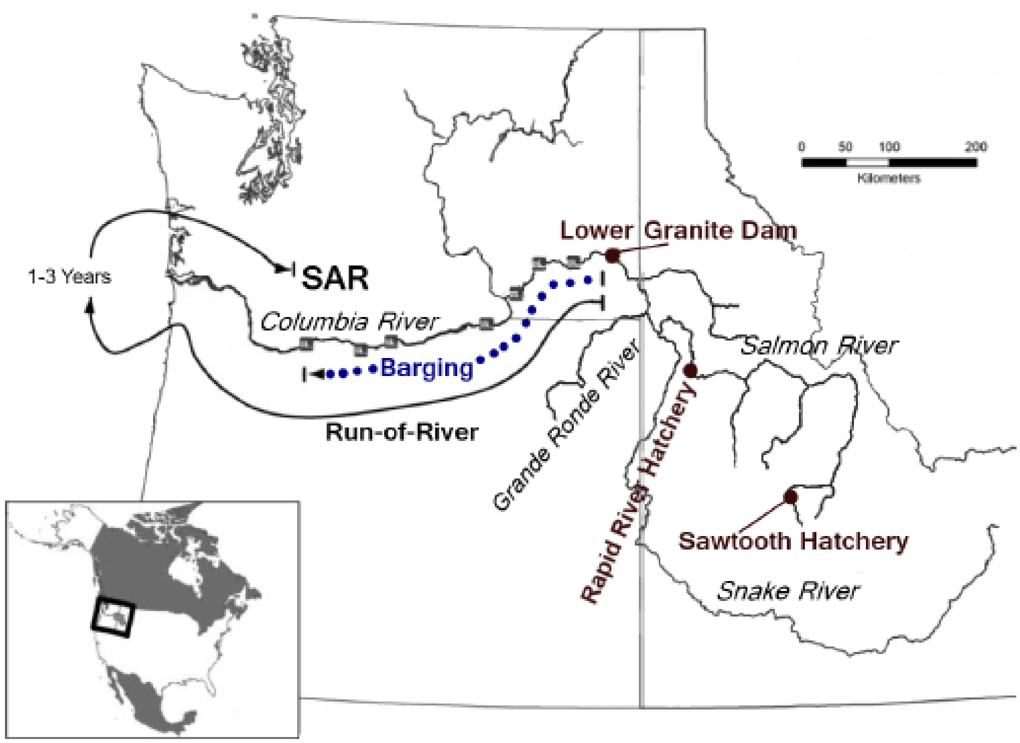

Fig. 1. Spring Chinook salmon freshwater survival calculated as movement from Sawtooth and Rapid River hatcheries to detection at Lower Granite Dam. Ocean survival (SAR) calculated from fish detected as juveniles at Lower Granite Dam and as adults returning to Bonneville Dam 1 to 3 years later. Ocean survival was estimated for fish passing through the hydrosystem in barges or in the river.

Table 2. Spring Chinook salmon PIT-tagged at Lower Granite Dam as juveniles and recovered as adults at Bonneville Dam.

	Wild Fish				Hatchery Fish			
	Barge #	SAR(%)	River #	SAR(%)	Barge #	SAR(%)	River #	SAR(%)
1999	8119	2.35	11829	1.39	43169	2.16	61478	1.49
2000	0		58496	1.77	0		0	
2001	17506	1.01	0		0		0	
2002	4899	1.47	33935	1.03	0		0	
2003	7101	0.42	43051	0.17	0		0	
2004	11194	0.54	0		0		0	
2005	12668	0.31	0		0		36094	0.09
2006	19505	0.91	10095	0.77	33935	0.81	148258	0.57
2007	16752	1.10	14513	0.68	23935	1.02	78111	0.24
2008	19022	3.25	9412	1.77	42452	2.36	98288	1.22
2009	13315	0.98	13815	0.43	0		91253	0.41

The model parameters k_0, k_1, x_c, and σ were estimated for individual years using the binary return data with a maximum likelihood estimator (mle2 function in the bbmle package in R; http://cran.us.r-project.org/). The survival curves were generated by parameters estimated from the binary data (Figs. 2-6). Survivals calculated by binning data over length increments were plotted on the figures for comparison purposes.

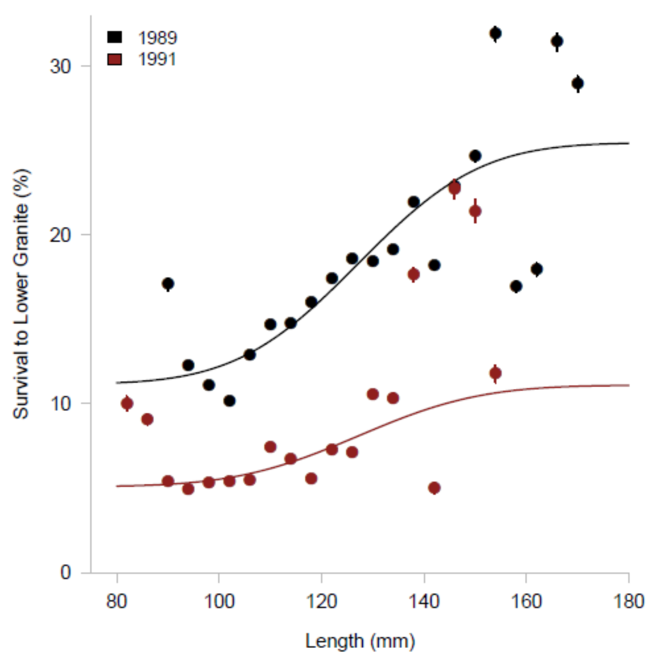

Fig. 2. Sawtooth Hatchery spring Chinook salmon survival for 1989 and 1991. Each point represents survival estimated by length bins. Curves were determined with the maximum likelihood estimator (mle2 function) of the binary data.

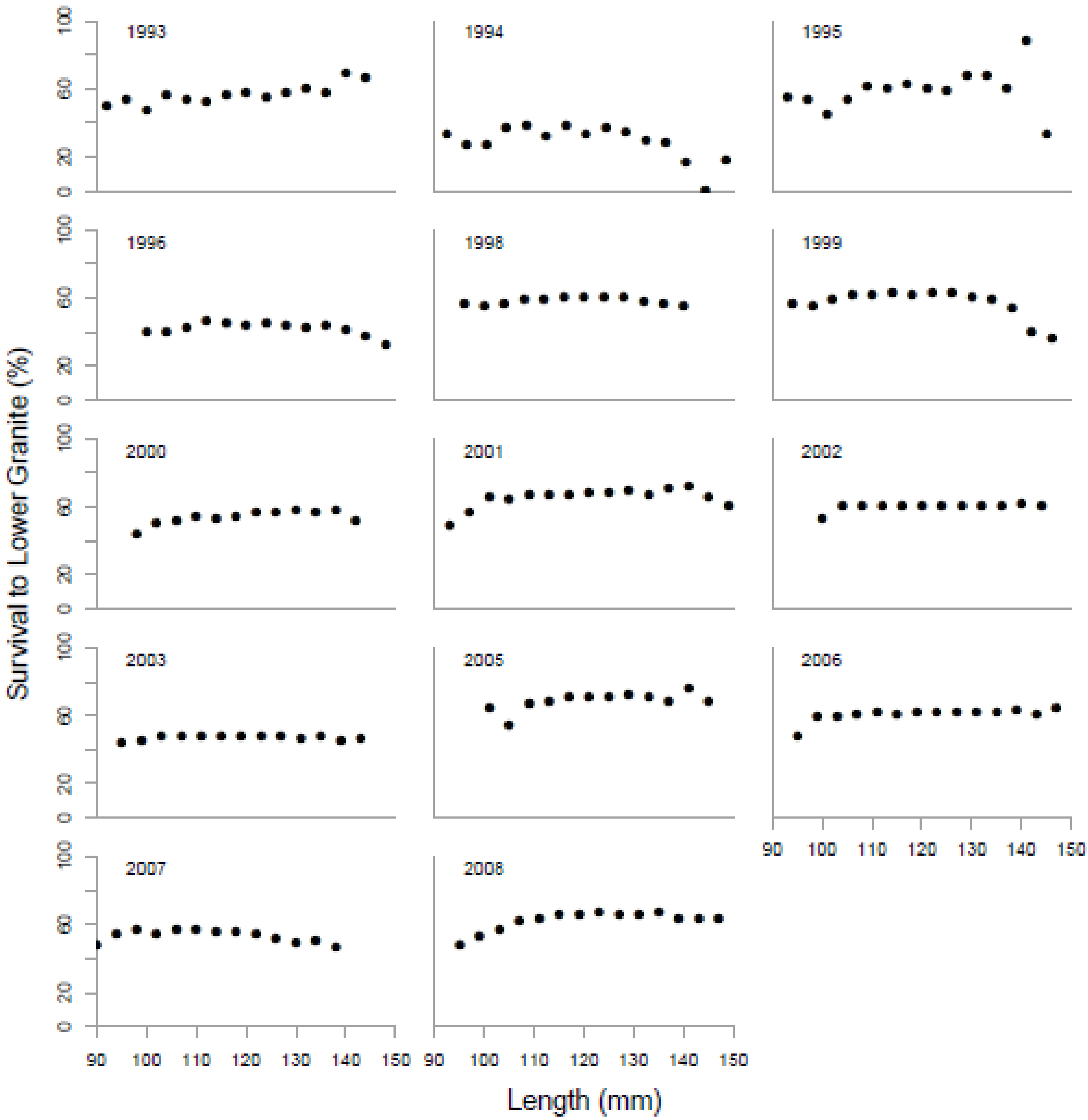

Fig. 3. Survival of Rapid River Hatchery juvenile spring Chinook salmon to Lower Granite Dam versus fish length.

Survival of Sawtooth Hatchery juvenile fish to Lower Granite Dam exhibited a clear size-dependent pattern but the level of mortality was different between years (Fig. 2). Survival of Rapid River Hatchery juvenile fish to Lower Granite Dam did not exhibit a clear size-dependent pattern (Fig. 3).

Size frequency distributions of fish PIT tagged for ocean survival varied between tagging years and were significantly different for the wild and hatchery fish. Wild fish mean length was about 110 mm while hatchery fish length was about 140 mm (Fig. 4).

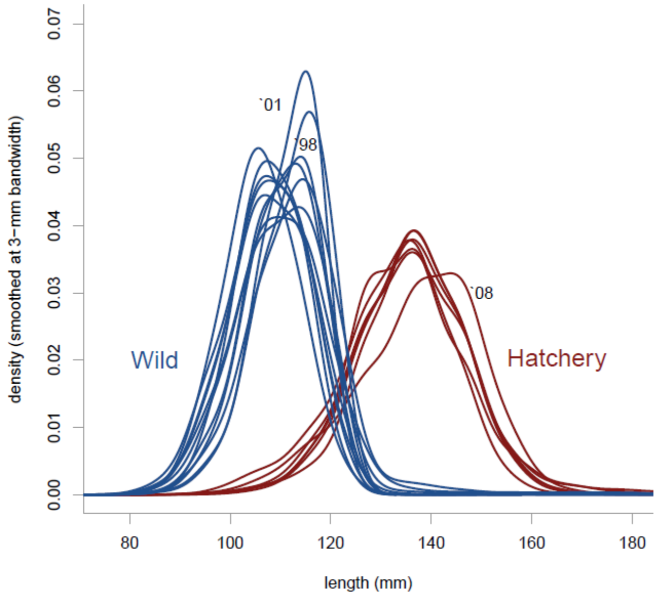

Fig. 4. Length distributions of wild and hatchery spring Chinook salmon tagged at Lower Granite Dam (1999–2009). A 3-mm bandwidth smoother was applied to eliminate extraneous noise.

In general for the ocean group, a strong size-dependent survival pattern was observed for all stocks. Figure 5 illustrates the survival pattern for the 2008 release year. For hatchery fish, which were longer than wild fish, the mean size of susceptibility was larger ($x_c \sim 140$ mm) than for the wild fish ($x_c \sim 100$ mm). Additionally, the barged fish exhibited a larger range of size variability than did the run-of-river fish.

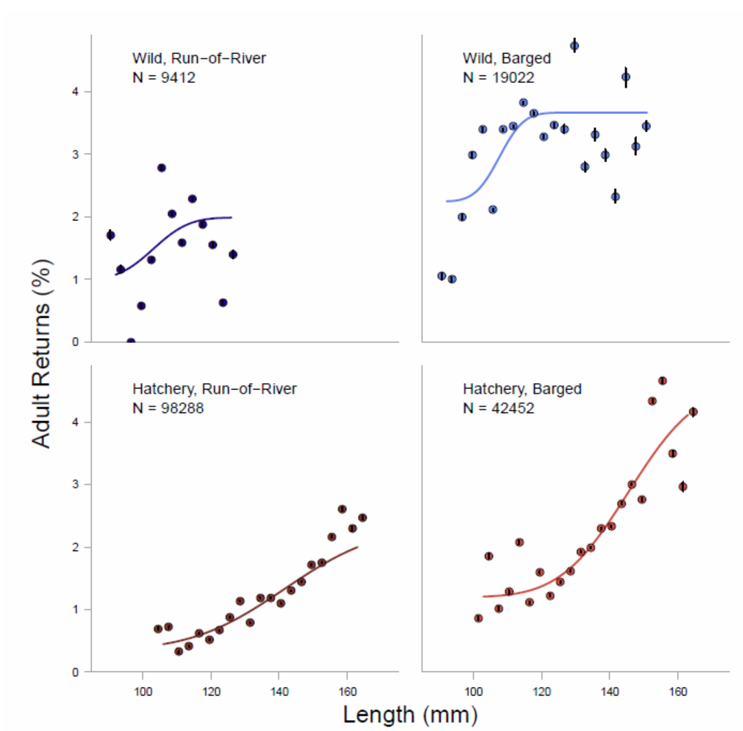

Fig. 5. Model fit of adult returns (%) to body length of the ocean group of hatchery and wild spring Chinook salmon released at Lower Granite Dam in 2008. Chinook salmon were either barged or swam in-river through the hydrosystem.

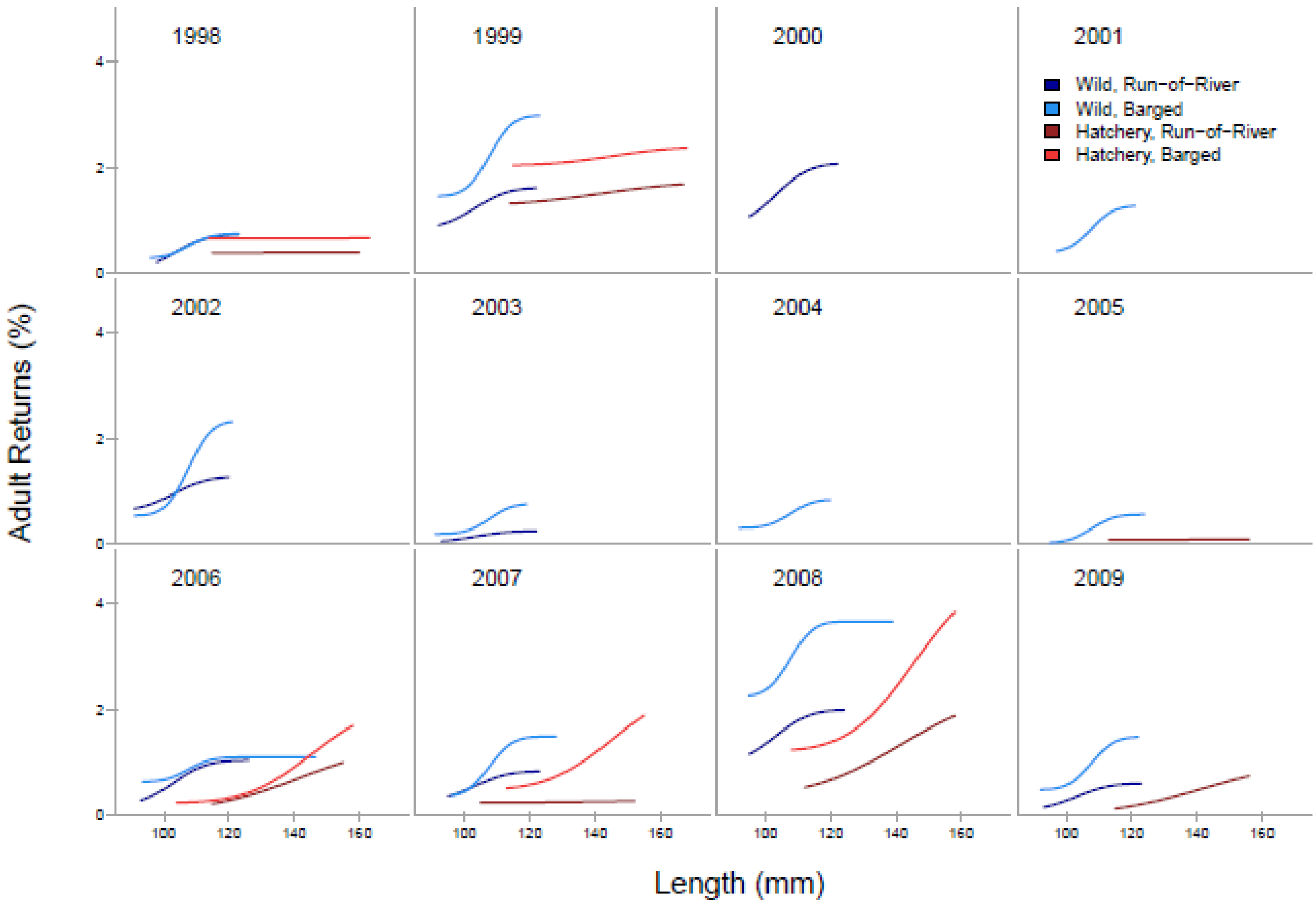

Fig. 6. Model fit of adult returns (%) to releases at Lower Granite Dam, 1998-2009. The model was fit to each run type, k_0 and k_1 allowed to vary by year, and the x_c and σ parameters were constant within each group across years.

Effect of size on ocean survival over all years of data is illustrated in Fig. 6 for wild and hatchery fish traveling by run-of-river and barged passage routes through the hydrosystem. A size effect is prevalent in most datasets, especially in wild fish that are barged.

Table 3. Summary of spring Chinook salmon parameter estimates for Lower Granite Dam data.

Run type	River passage	Mean length (mm)	x_c	x_c lower 95%	x_c upper 95%	σ	σ lower 95%	σ upper 95%
Wild	Barge	110.5	107.6	106.3	109.0	5.6	4.2	7.6
Wild	Run-of-river	109.1	103.1	101.0	105.2	8.2	5.9	11.5
Hatchery	Barge	136.2	145.5	141.0	150.2	15.7	12.6	19.6
Hatchery	Run-of-river	135.6	141.6	138.0	145.3	21.4	18.3	24.9

Summary statistics of model parameters x_c and σ for the ocean group are given in Table 3. The mean lengths of wild fish are slightly larger than the mean critical length estimates, falling outside the 95% confidence interval. The mean lengths of hatchery fish fall below the x_c confidence interval. In general, the size selection of wild and hatchery fish were different and corresponded with the mean size of the respective groups.

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