

Falling behind: delayed growth explains life-history variation
in Snake River fall Chinook salmon

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1 **Abstract**

2 Fall Chinook salmon typically migrate to the ocean as age-0 subyearlings, but the appearance
3 of a strategy whereby juveniles over-winter in freshwater and migrate to the ocean as age-1
4 yearlings has arisen over the past few decades in Idaho's Snake River population. The recent
5 appearance of the yearling strategy has conservation implications for this threatened population
6 because of survival and reproductive differences between the two life histories. Different
7 proportions of juveniles adopt the yearling life history in different river reaches and years, and
8 temperature differences are thought to play some role in accounting for this variation. The specific
9 circumstances under which juveniles pursue this life history are poorly understood. We advance a
10 hypothesis for the mechanism by which juveniles adopt a life history, formalize it with a model,
11 and present the results of fitting this model to life-history data. The model captures patterns of
12 variation in yearling proportions among reaches and years and appears robust to uncertainty in a
13 key unknown parameter. From fitting the model to empirical yearling proportions, our results
14 suggest that juveniles commit to a life history earlier in development than the time at which
15 smoltification typically begins. Specifically, juveniles that become yearlings do so soon after
16 emergence if they are too far behind a typical growth schedule given temperature and photoperiod
17 cues at that time. Our model also offers those interested in the management and conservation of
18 Snake River fall Chinook salmon a useful tool to account for life history variation in population
19 viability analyses and decision making.

20 Introduction

21 Pacific salmon display stunning variety in life history (Groot and Margolis 1991). Shaped by
22 millenia of change in an active geological setting, each species is partitioned into distinct
23 populations in time and space according to the time of year spawners migrate upriver and the
24 stream in which they spawn (Waples et al. 2008a). Variety in life histories exists within
25 populations, too. Adults may spend one to five years at sea or not go at all (Groot and Margolis
26 1991, Brannon et al. 2004), males may adopt alternative reproductive strategies (Koseki and
27 Fleming 2006, 2007), and juveniles may spend variable amounts of time rearing in oceans,
28 estuaries, or rivers (Connor et al. 2005, Koski 2009).

29 An important life-history dimorphism in the population of fall Chinook salmon (*Oncorhynchus*
30 *tshawytscha*) residing in the Snake River of Idaho and Oregon (Figure 1) is the amount of time
31 juveniles spend rearing in freshwater before migrating to the ocean. Individuals of the ‘subyearling’
32 life-history type undergo preparations for entry into the ocean (smoltify) and outmigrate at age 0
33 the summer after they hatch, whereas ‘yearlings’ over-winter in freshwater, smolting and migrating
34 to the ocean at age 1 the following spring (Connor et al. 2005). Until recently, it was believed that
35 all fall Chinook salmon exited freshwater as subyearlings, but as many as 84.6% of juveniles in
36 some Snake River tributaries migrated as yearlings in recent years (Connor et al. 2002). This shift
37 to a yearling life history appears to have taken place in the latter half of the 20th century and may
38 be explained by either an environmentally controlled or evolutionary response to spawning ground
39 displacement following dam construction (Connor et al. 2002, Williams et al. 2008).

40 The recent shift to the yearling life history has implications for the persistence of Snake River
41 fall Chinook salmon, which are considered threatened under the U.S. Endangered Species Act
42 (National Marine Fisheries Service 1995). Yearlings are thought to experience greater survival
43 than subyearlings during the survival bottleneck that occurs during ocean entry (Connor et al.
44 2005), but this survival advantage comes at the cost of forgoing rewarding opportunities for
45 growth in the more productive oceans and later suffering reduced fecundity as a future
46 consequence (Milks et al. 2009). Despite a possible tradeoff between survival and fecundity,
47 yearlings have higher smolt-to-adult return rates than subyearlings (Connor et al. 2005) and their
48 recent emergence may have contributed to the population’s demographic resurgence in the past

49 few years (Williams et al. 2008).

50 Given the substantial demographic differences between these life histories, understanding the
51 circumstances leading individuals to adopt one or the other has important implications for
52 projecting the population's future status. Unfortunately, our knowledge of what underlies this
53 life-history dimorphism is limited. Other life history variation in Pacific salmon, such as the
54 distinct behavior of fall and spring Chinook salmon, has a genetic component (Clarke et al. 1994,
55 Brannon et al. 2004). However, such a simple, purely genetic basis for the subyearling-yearling
56 dimorphism is unlikely because of marked spatial patterns in yearling proportions in different
57 reaches of the Snake River Basin (Connor et al. 2002) despite high gene flow (Garcia et al. 2004)
58 and genetic similarity (Narum et al. 2007). Even so, flexible, genetically-based differences are
59 thought to play a frequent and important role in salmonid life-history variation (Unwin et al.
60 2000, Carlson and Seamons 2008), so there is reason to suspect that they do for Snake River fall
61 Chinook salmon, too (Williams et al. 2008).

62 Another possibility is that juvenile life history is a conditional strategy, whereby the life
63 history an individual adopts depends on some measure of its state relative to a genetically
64 determined threshold state at some point during its early development (Hazel et al. 1990, 2004,
65 Tomkins and Hazel 2007). Conditional strategies thereby incorporate both environmental factors
66 (which influence the individual's state) and genetics (which underlies the threshold state). An
67 individual's state can sometimes be influenced by genetics, too, such as if it has a genetically
68 determined growth rate. Among salmonids, conditional strategies have been invoked to explain
69 alternative maturation schedules in Atlantic salmon (*Salmo salar*) (Myers et al. 1986,
70 Aubin-Horth and Dodson 2004, Aubin-Horth et al. 2006, Thorpe et al. 1998), reproductive
71 strategies in male coho salmon (*O. kisutch*) (Koseki and Fleming 2006, 2007), and anadromy
72 versus residency in steelhead (*O. mykiss*) and Arctic and brook charr (*Salvelinus alpinus*, *S.*
73 *fontinalis*) (Rikardsen et al. 2004, Theriault et al. 2007, Satterthwaite et al. 2009*a,b*).

74 The strategies of initiating or postponing smoltification at a particular time are thought to
75 depend most strongly on temperature and day of year (DOY) (a proxy for photoperiod) (Hoar
76 1976, Wedemeyer et al. 1980). On the one hand, temperature seems to affect smoltification timing
77 contingent upon individual status (Zaugg and McLain 1976) and to play a role in stimulating

78 outmigration (Sykes et al. 2009). On the other hand, smoltification only occurs within a certain
79 window of time as sensed by photoperiod cues (Hoar 1976). Furthermore, there is evidence of an
80 interaction between photoperiod and size cues for triggering smolting in Chinook salmon
81 (Beckman et al. 2007). We propose that once the process of smoltification has been initiated by
82 whichever of a temperature or DOY threshold is detected first, juvenile Snake River fall Chinook
83 salmon that exceed a threshold length adopt a subyearling life history while those smaller than the
84 threshold adopt a yearling life history. The influence of temperature and photoperiod could be
85 incorporated in the model in other ways (e.g., Sykes et al. 2009), but in the absence of more
86 detailed knowledge thresholds are a useful and straightforward way to account for the effects of
87 temperature and photoperiod on the elicitation of smoltification and outmigration behavior.

88 In this study, we postulate a model in which juvenile life history of Snake River fall Chinook
89 salmon is determined as a conditional strategy. We optimized this model to determine what values
90 of genetically determined length, temperature, and DOY thresholds lead to yearling proportions
91 most consistent with empirical estimates by Connor et al. (2002). We also evaluated model
92 performance and its sensitivity to these three parameters, as well as emergence timing and length
93 at emergence. Finally, we ask how different assumptions about over-winter survival, which in turn
94 lead to different interpretations of the data, influence the choice of threshold values most
95 consistent with empirical patterns.

96 **Methods**

97 *Simulation Model*

98 The conceptual model we adopt is that juveniles pursue either the subyearling or yearling life
99 history depending on their fork lengths relative to a threshold length once life-history
100 differentiation is cued by temperature or DOY (Figure 2). If their fork length exceeds the length
101 threshold they smoltify and outmigrate, and if it does not they over-winter in freshwater. We
102 formalized this conceptual model with simulations that track the daily progression of fry from
103 individual redds (nests) until the time at which either the temperature or DOY threshold is
104 triggered. Temperature-dependent growth and temperature- and length-dependent survival were
105 evaluated daily for each redd. We carried out these simulations using temperature data from three

106 reaches (Clearwater River, lower and upper Snake River) (Figure 1) and several years (1991-1997,
107 1999) for which empirical yearling proportions were available. Yearling proportions from these
108 simulations form the basis of our analysis.

109 *Spawning.*—The first step in the simulations was assigning each redd a spawning date from the
110 empirical distribution of spawning dates in the upper and lower mainstem Snake River for the
111 years 1991-2006 and the Clearwater River for 2001-2006. Within each river and year, regular
112 aerial surveys recorded the number of new redds created since the last survey (for a detailed
113 explanation of survey methods see Garcia et al. 2004). For each river and year, we fitted a normal
114 cumulative density function to the cumulative number of redds through time by minimizing the
115 sum of squared deviations. Because complete data were not available for all years and reaches, we
116 used averages of available spawning times for each reach (mean DOY \pm SD): Clearwater
117 (307.78 \pm 13.06), lower Snake (310.65 \pm 10.5), upper Snake (308.09 \pm 7.67). In the simulations, we
118 randomly drew spawning dates from these fitted distributions and initiated juvenile development
119 in each redd on those dates. Randomness of spawning dates among redds is the primary source of
120 stochasticity in our model.

121 *Temperature.*—Daily mean water temperature data for the years 1991-2006 were provided by
122 Idaho Power Company for the mainstem Snake River (lower and upper reaches) and for the lower
123 Grande Ronde River. We obtained water temperature data from the US Geological Service
124 website (<http://waterdata.usgs.gov/nwis/sw>) for two gages on the lower Clearwater River (Station
125 Numbers 13341050 and 13342500). We used all gages for daily temperature imputation but only
126 the Snake River gages and the Clearwater's Peck gage in the simulation model because of their
127 proximity to the primary spawning areas. Daily mean temperature readings from gages like these
128 have been shown to correlate strongly with daily mean temperatures in artificial Chinook salmon
129 redds in the Snake River (Groves et al. 2008), suggesting that they are applicable to our model of
130 egg and alevin development. We also apply these temperature readings to our model of fry
131 because the model assumes that fry remain in their natal streams for the period of time
132 considered in our model (i.e., up to life history differentiation but not after).

133 For days with missing average daily water temperatures, values were imputed from averages
134 reported for the same day at other sites. For each site, linear relationships between daily mean

135 temperatures from different gages were fitted between all pairs of gages (Table 1). We identified
136 one primary relationship for each site as the site with the strongest relationship. After imputing
137 temperatures based on the primary relationship, the remaining missing values were imputed using
138 a secondary relationship with the highest temporal overlap with missing data. This procedure was
139 sufficient to impute missing temperatures at all five sites. The relationships were generally strong
140 ($0.77 \leq R^2 \leq 0.97$). A combination of empirical and imputed temperature data from the
141 Clearwater River and the lower and upper Snake River were then used in the model (Figure 3).

142 *Egg and Alevin Development and Survival.*—Simulation of juvenile recruitment in each
143 spawning area relied on the assumption that development of early life stages was largely controlled
144 by accumulated thermal units, °C (ATU). We assumed that extreme temperatures (less than zero
145 or greater than 30°C) did not contribute to juvenile development. We estimated the influence of
146 temperatures less than 5°C to be half of the actual temperature (Alderdice and Velsen 1978,
147 Beacham and Murray 1989).

148 Two laboratory studies (Murray and McPhail 1988, Geist et al. 2006) and one field study
149 (Connor and Burge 2003) of fall Chinook salmon from the northeastern Pacific Ocean estimated
150 the number of thermal units required for 50% of fertilized eggs to hatch and for 50% of alevins to
151 develop into fry and emerge from redds. Geist et al. (2006) reported that 535 ATU were required
152 to hatch and another 409 ATU to reach emergence (944 ATU total), which is consistent with the
153 findings of Murray and McPhail (1988). Connor and Burge (2003) reported that 1066 ATU were
154 required for emergence under field conditions due to extra time required for fry to emerge from
155 gravel covering the redd. We conducted distinct sets of simulations using the assumptions of
156 either 944 or 1066 ATU for emergence to test whether our model and the best-fit parameter values
157 were robust to uncertainty in the ATU threshold for emergence. We also conducted simulations in
158 which individuals possessed variation in ATU thresholds for emergence. For those simulations, we
159 assumed that ATU thresholds for emergence were normally distributed among individuals with a
160 mean of either 944 or 1066 ATU and a standard deviation of 63.44 ATU, which was estimated
161 from data provided by B. Bellgraph and G. McMichael (McMichael et al. 2005).

162 To estimate daily survival of eggs and alevins as a function of daily mean temperature, we
163 fitted curves to daily survival estimates of eggs and alevins from six published studies (Combs and

164 Burrows 1957, Heming 1982, Garling and Masterson 1985, Murray and McPhail 1988, Beacham
 165 and Murray 1989, Jensen and Groot 1991). These studies took place in laboratories at constant,
 166 but differing temperatures ranging 1.583 – 20 °C. These studies reported survival during the
 167 periods between egg fertilization and hatching and between hatching and emergence, so to obtain
 168 estimates of daily survival we raised survival over each period to the $\frac{1}{d}$ power, where d is the
 169 duration of each period in days. Because some studies did not report the duration of these
 170 periods, we fitted the duration of each period as a function of incubation temperature and used
 171 the resulting fitted values of d . We then fitted daily survival as a function of daily mean
 172 temperature for each period to obtain

$$\text{daily egg survival} = \left(1 - e^{-(\text{temperature}/1.879)^{1.234}}\right) e^{-(\text{temperature}/17.43)^{65.46}} \quad (1a)$$

$$\text{daily alevin survival} = \left(1 - e^{-(\text{temperature}/0.4240)^{1.540}}\right) e^{-(\text{temperature}/16.02)^{75.82}} \quad (1b)$$

173 by least squares using the ‘optim’ function in R (R Development Core Team 2009).

174 *Fry Growth and Survival.*—We assumed that temperature differences among reaches and years
 175 explain most variation in juvenile growth. We accounted for temperature-dependent growth in
 176 simulations by adding a daily growth increment consistent with each day’s temperature. The
 177 relation between temperature and daily growth from a study of juvenile Snake River fall Chinook
 178 salmon was daily growth ($\text{mm} \cdot \text{d}^{-1}$) = $0.184 + 0.077 \times \text{temperature} (\text{°C})$ (Connor and Burge
 179 2003).

180 Upon emergence, fry were assumed to have a fork length of either 30.7 (Murray and McPhail
 181 1988) or 35.2 mm (Geist et al. 2006). We conducted distinct sets of simulations to test whether
 182 our model and the best-fit parameter values were robust to uncertainty in fork length at
 183 emergence. We also carried out simulations in which individuals possessed variation in fork length
 184 at emergence by assuming that this quantity was normally distributed among individuals with a
 185 standard deviation of 1.75 mm. Because the ATU threshold for emergence was also variable in
 186 these simulations, the deterministic component of an individual’s fork length at emergence was a
 187 function of the difference between that individual’s ATU threshold for emergence and the mean
 188 threshold: a linear function with slope 4.58×10^{-3} and intercept of either 30.7 or 35.2 mm.

189 Parameters for the inclusion of variation in fork length at emergence were estimated from data
190 provided by B. Bellgraph and G. McMichael (McMichael et al. 2005).

191 Survival of fall Chinook fry is known to depend strongly on size. Data consistent with this
192 come from a study by Connor et al. (2004) in which they released PIT-tagged fry at different
193 lengths and recorded their survival upon passage of Lower Granite Dam. To translate survival
194 between release and passage at the dam, which occurred over several weeks, to an estimate of
195 daily survival, we fitted data from Connor et al. (2004) to obtain the relationship

$$\text{daily fry survival} = 0.99 - (0.99 - 0.96)e^{-(\text{FL}/91.445)^{100}}, \quad (2)$$

196 where FL is fork length in mm. Fitted parameter values in Eqn. (2) differed based on assumptions
197 about the ATU threshold for fry emergence and fork length at emergence, but fitted values were in
198 agreement to the precision in Eqn. (2) and $R^2 > 0.98$ in all cases. Details of the procedure used to
199 obtain this formula are presented in the Appendix.

200 *Threshold Parameter Estimation*

201 To determine which combination of threshold parameter values produced simulated yearling
202 proportions most consistent with observations, we searched for a best-fit parameter combination
203 that minimized

$$\text{SSQ}(D, S, T) = \sum_{\forall t, x} (\text{sim}(t, x; D, S, T) - \text{emp}(t, x))^2,$$

204 the sum of squared differences (SSQ) between simulated and empirically estimated yearling
205 proportions summed over all years t and reaches x . Quantitatively, $\text{SSQ} = 0$ implies a perfect
206 correspondence between simulated and empirically estimated yearling proportions, $\text{SSQ} = 1.31$
207 when all simulated juveniles become subyearlings, $\text{SSQ} = 12.61$ when all simulated juveniles
208 become yearlings, and $0 < \text{SSQ} < 12.61$ when simulated juveniles are a mixture of life histories. To
209 search for the best-fit parameter combination, we conducted a global optimization by complete
210 enumeration. Specifically, we considered every other integer DOY D in the range 121 to 273,
211 lengths L of 31 to 150 mm incremented by 2 mm, and temperatures T of 12 to 22° C incremented
212 by 0.5° C.

213 *Over-winter Survival*

214 Connor et al. (2002) reported the proportion of yearling migrants recorded passing Lower
215 Granite Dam. Their definition of yearling proportion p is

$$p = \frac{y}{s + y},$$

216 where s and y are the number of subyearlings and yearlings recorded passing Lower Granite Dam
217 from the same cohort. More precisely, s is the number of PIT-tagged fish released in year t that
218 pass Lower Granite Dam in year t , and y is the number of PIT-tagged fish released in year t that
219 pass Lower Granite Dam in year $t + 1$.

220 To estimate the proportion of juveniles p' initially adopting a yearling life history in the first
221 place, we first noted that the initial number of subyearlings $s' = s$ and yearlings $y' = y/u$, where u
222 is the survival of yearlings once they commit to that life history and before they pass Lower
223 Granite Dam (hereafter ‘over-winter survival’). It follows that the proportion p' is

$$p' = \frac{y'}{s' + y'},$$

224 which can be written in terms of the empirically estimated proportion p and unknown over-winter
225 survival u as

$$p' = \left(1 - u + \frac{u}{p}\right)^{-1}. \quad (3)$$

226 Over-winter survival u accounts for mortality risks posed over a period of several months in
227 potentially harsh environments. Because $u < 1$ could mean that p' and p are quite different, we
228 explored how u affects p' for empirically estimated values of p . Moreover, because a primary goal
229 of our investigation was to estimate values for the thresholds underlying the decision to adopt one
230 life history or the other, we determined the sensitivity of the thresholds to u by exploring how
231 relative differences in SSQ among different threshold parameter values change with a range of u
232 values (1, 0.75, 0.5, 0.25).

233 Results

234 We identified the following thresholds as those best matching empirically estimated life-history
235 proportions under the assumption of zero over-winter mortality: DOY threshold of
236 $D^* = 167 - 211$, length threshold of $L^* = 35 - 48$ mm, and temperature threshold of $T^* = 14.0^\circ\text{C}$
237 (Table 2). This range of best-fit values is underlied by uncertainty in the ATU threshold for
238 emergence, fork length at emergence, and the existence of individual variation in those quantities.
239 Despite uncertainty in these parameters, some generalities about the best-fit values are that (1)
240 the DOY threshold is so great as to make it inapplicable in most reaches and years, (2) whenever
241 the DOY threshold triggers life-history differentiation it does so no more than 10 days before a
242 temperature threshold is triggered, (3) the length threshold is only 5-13 mm greater than fork
243 length at emergence, and (4) the temperature threshold is always 14.0°C . In all subsequent
244 analyses, we focus on the set of best-fit thresholds of $D^* = 177$, $L^* = 40$, and $T^* = 14$ (fourth
245 column of Table 2), as these correspond to the most realistic scenario about the ATU threshold for
246 emergence and fork length at emergence under field conditions.

247 Of the two possible triggers (i.e., DOY or temperature), the temperature threshold always
248 occurred first given the best-fit parameters (from left to right, daily mean temperatures exceed the
249 horizontal lines before DOYs exceed the vertical lines in Figure 3). Because it was never triggered,
250 goodness of fit was insensitive to the DOY threshold, as any $D > 175$ provided as good a fit as D^*
251 (flat goodness of fit profile for $D > 175$ in Figure 4a). In contrast, L^* and T^* provided uniquely
252 good fits (distinct global minima at L^* and T^* in Figure 4b,c). Length and temperature
253 thresholds far from L^* and T^* provided unreasonable fits to empirical yearling proportions at
254 Lower Granite Dam, as indicated by high SSQ outside the region $35 \text{ mm} < L < 45 \text{ mm}$, 14°C
255 $< T < 15^\circ\text{C}$ (gray and white in Figure 5a). Length thresholds smaller than 35 mm and
256 temperature thresholds greater than 15°C caused all juveniles to become subyearlings (maximum
257 $\text{SSQ} = 1.31$), whereas length thresholds exceeding 45 mm and temperature thresholds less than
258 14° caused all juveniles to adopt the yearling life history (maximum $\text{SSQ} = 12.61$) (Figure 4b,c).
259 The best-fit threshold parameter values produced $\text{SSQ} = 0.2341$.

260 Applying best-fit threshold values to the model generated yearling proportions that were
261 mostly in the vicinity of empirically estimated proportions (Table 3) and accounted for 74% of the

262 variance among yearling proportions estimated by Connor et al. (2002) ($R^2 = 0.7409$). This
263 compares favorably to mean annual stream temperature as a predictor of empirical yearling
264 proportions, which accounts for only 40% of the variance (Connor et al. 2002). Applying best-fit
265 parameter values to the model also did a good job of identifying the rank order of yearling
266 proportions in the Clearwater River, and it correctly identified which year saw the most yearlings
267 in the lower Snake River (Table 3). It did a poorer job of identifying the correct rank order for the
268 other observations, as overall concordance between simulated and empirical yearling proportions
269 was not significant (Kendall's $\tau=0.2611$, $p = 0.09$). Although simulated proportions did not match
270 empirical estimates in several years in the Snake, means and variation across years were similar
271 within reaches for the years in which observations were made (1991-1997, 1999) (Table 4).
272 Applying the model to unpublished data for 2000-2005 in the Snake River was less successful,
273 yielding simulated proportions higher than observations (Table 4). Most of this difference is
274 attributable to a single high-yearling simulation result between 2000 and 2005 in each of the lower
275 and upper Snake.

276 Acknowledging that some over-winter mortality is bound to occur (i.e., $u < 1$) means that the
277 the proportion of fry that adopt a yearling strategy in the first place will always exceed the
278 proportion of yearling migrants passing Lower Granite Dam a year later (Figure 6). Reliable
279 estimates of over-winter survival are lacking, but Williams et al. (2008) considered values of 0.2 to
280 0.8 in their analysis and Muir et al. (1999) assumed a value of 0.65. If survival is on the lower end
281 of this range, then in some reaches and years as many as two- to three-fold more may have
282 over-wintered than were estimated at Lower Granite Dam (Figure 6). Although over-winter
283 mortality alters expectations about the proportion of fry that should adopt a yearling strategy in
284 the first place, we found that it did not noticeably change which length and temperature
285 thresholds best explained life history variation across reaches and years. Length thresholds of
286 35-45 mm and temperature thresholds of 14-15°C produced the best match to proportions
287 estimated at Lower Granite Dam for u ranging 0.25 – 1 (overall similarity of a-d in Figure 5).
288 Because best-fit thresholds were insensitive to a range of values of u , it is reasonable to assume
289 that year-to-year variation in overwinter survival would also have little effect on best-fit thresholds.

290 Discussion

291 In this study, we advanced a hypothesis for the mechanism by which juvenile fall Chinook
292 salmon in the Snake River adopt one of two life histories, and we formalized that hypothesis with
293 a model. The model integrated published information about temperature-based growth and
294 survival with daily mean temperatures to simulate individual growth trajectories commencing on
295 a known distribution of spawning dates. Simulated growth trajectories and daily temperature
296 data allowed us to evaluate a range of threshold trait values to determine which values produced
297 simulated yearling proportions most consistent with empirical estimates. Indeed, best-fit threshold
298 parameters produced simulated proportions consistent with both empirical estimates and known
299 temperature differences among river sections and observation years. Furthermore, we determined
300 that best-fit threshold parameters were robust to uncertainty in a number of parameters, including
301 the ATU threshold for emergence, fork length at emergence, and yearling over-winter survival.

302 *Empirical Corroboration of Best-Fit Thresholds*

303 A surprising result is how early our model suggests that life-history differentiation occurs.
304 Model results suggest that juveniles pursuing a yearling life history commit to that trajectory
305 shortly after emergence if temperatures are high enough or DOY late enough, which is much
306 earlier than when smoltification begins. This finding is consistent with life history differentiation
307 in Atlantic salmon, wherein a commitment to mature one year or the next depends on an
308 individual's state well in advance of maturation (Myers et al. 1986, Thorpe et al. 1998). The
309 result that life-history differentiation of Snake River fall Chinook salmon occurs prior to the onset
310 of smoltification suggests that little scope exists for altering life history after emergence. Several
311 empirical studies support the plausibility of this result.

312 The timing of downstream movement from natal streams is one piece of evidence that
313 supports the hypothesis of life-history differentiation shortly after emergence. Working backwards,
314 if outmigrating subyearlings vacate Lower Granite Reservoir by around July 19 (Curet 1993) and
315 if juveniles spend 38-57 days rearing there before continuing migration (Connor et al. 2003), then
316 juveniles probably depart their natal streams sometime in late spring. This timeline is consistent
317 with our best-fit temperature threshold of 14 °C, which was first triggered around June 8 (DOY

318 159) on average (range of 141-183).

319 The best-fit temperature threshold of 14°C is also corroborated by these studies. First, Curet
320 (1993) found that temperatures reaching 18°C correlated with most salmon departing from Lower
321 Granite Reservoir and moving downstream, so a temperature cue for leaving the natal stream
322 should logically be somewhat less because juveniles leave their natal streams weeks before
323 temperatures get that high (Connor et al. 2003). Second, in an effort to forecast survival between
324 natal streams and Lower Granite Dam, Connor et al. (2000) found that survival during this time
325 was maximized when juveniles initiated downstream movement from their natal streams at 14°C.
326 The best-fit temperature threshold, also 14°C, therefore appears adaptive and could have been
327 selected for over time.

328 Experiments could be devised to more directly test the model results in a design that exposes
329 PIT-tagged groups of hatchery individuals to set thermal regimes and size distributions and later
330 determines the proportion of yearlings from each group. Comparisons of these groups could be
331 used to test our hypothesis of life-history differentiation following emergence and to empirically
332 quantify length and temperature thresholds.

333 *Smolting: Incitation or Reversal?*

334 Instead of using environmental cues and individual state as a trigger for inciting the
335 smoltification and outmigration process, these signals might trigger a reversal of their advance
336 toward smoltification. The smoltification process has been shown to reverse under high
337 temperatures in a laboratory setting (Clarke and Blackburn 1977). Furthermore, at the time when
338 life history differentiation occurs in our model (i.e., once a day's mean temperature exceeds
339 14 °C), most juveniles that become subyearlings far exceed the length threshold of 40 mm
340 (Figure 7). In fact, most are 50-70 mm by this time, and Chinook salmon juveniles of this size
341 have typically already begun offshore movement, downstream migration, and will soon take up a
342 period of residence in Lower Granite Reservoir (Connor et al. 2003). Thus, alevins and newly
343 emerged fry are likely so far behind a typical growth schedule at that point that it is more
344 adaptive to reverse their advance toward smoltification, over-winter in freshwater, and migrate as
345 a yearling than to pursue the typical subyearling migration course.

346 The hypothesis that developing juveniles reverse course if they fall behind a typical, adaptive

347 growth schedule allows for the possibility of multiple opportunities over a fish's development for
348 such a reversal of course. Additional opportunities for over-wintering beyond the 14°C threshold
349 could account for several instances where the model predicts fewer yearlings than were empirically
350 estimated. Specifically, in the lower Snake River in 1992, 1996, and 1999, the size distribution at
351 the time 14°C was first experienced is quite far ahead of where it should be to produce empirically
352 estimated yearling proportions (Figure 7). However, if growth thereafter is slowed by cool
353 temperatures or lack of food, some of those fish may fall behind the typical, adaptive growth
354 schedule and opt to over-winter once another temperature or DOY threshold is reached, thus
355 accounting for those who were counted as yearlings. That these decisions could potentially be
356 made at any point during downstream migration is consistent with the hypothesis that some
357 juveniles might decide to over-winter later on at any number of reservoirs between Lower Granite
358 Dam and the ocean (Connor et al. 2002, Buchanan et al. 2009). Although it may be more realistic
359 to say that individual growth is assessed against multiple thresholds at multiple checkpoints during
360 development, our results support the hypothesis that life-history differentiation occurs once: soon
361 after emergence. Empirical yearling proportions for reservoirs downstream of Lower Granite Dam
362 could help determine whether such a 'wait and see' strategy occurs by similar means as the 'decide
363 early' strategy we propose, but data to test that hypothesis are not currently available.

364 *Demographic Implications*

365 One of the primary motivations for research on juvenile life history of Snake River fall Chinook
366 salmon is its relevance to the recent resurgence and hopeful recovery of this population (Williams
367 et al. 2008). Maximizing the utility of our model for managers will therefore require integrating it
368 within a population viability analysis (PVA). Such an effort could shed light on the impacts of
369 different degrees of life history variation on extinction risk of this population, telling us whether
370 the increased prevalence of yearlings will benefit the population and what the implications of
371 management actions are that affect life histories via temperature change. Given that our model
372 provides a reasonable description of yearling proportions within a reach averaged over time
373 (similarity between simulated and empirical mean +/- SE in Table 4), it is suitable for application
374 to PVA, where accounting for long-term variation supercedes year-to-year prediction.

375 An important consideration for the management of any species over the next several decades is

376 climate change. Some of the changes anticipated for the interior Pacific Northwest that could
377 affect spawning and rearing areas in the Snake River Basin include milder winters and overall
378 higher surface air temperatures, which are in turn likely to effect a rise in stream temperatures
379 (Crozier et al. 2008). Per our results, climate change might affect this population's life history in
380 either of two ways. On the one hand, milder winters would lead to earlier emergence, earlier
381 exceedance of the length threshold, and thus fewer yearlings. On the other hand, yearling
382 percentages could increase if the temperature threshold is exceeded earlier in the spring.
383 Complicating matters further, impacts of climate change on other aspects of life history could also
384 alter juvenile life history. Perhaps most importantly, changes in spawning date, which tends to be
385 extremely labile and heritable (Carlson and Seamons 2008), could increase or decrease yearling
386 percentages or possibly even buffer life history changes promoted by milder winters and
387 unseasonably high temperature extremes.

388 Another factor that may influence the future life history of this population is hydropower
389 (Waples et al. 2008*b*). Changes in temperature and flow regimes from hydropower manipulation
390 have generated marked selection pressures on Chinook salmon in Oregon (Angilletta et al. 2008),
391 make possible over-summer residence in Lower Granite Reservoir due to summer flow
392 augmentation (Connor et al. 2003, Smith et al. 2003), and could exert additional influence in the
393 future if dams are ever removed or abandoned (Williams et al. 2008). In fact, the population's
394 displacement from its historical spawning grounds due to dam construction is believed to have
395 instigated the shift towards more yearlings in the first place (Connor et al. 2002, Williams et al.
396 2008). Both cooler temperatures and lower food availability may have contributed to this abrupt
397 life-history shift (Connor et al. 2002, Williams et al. 2008). In future work, our model could be
398 used to investigate the role of temperature differences between historic and present-day reaches in
399 accounting for more yearlings in the latter. In its present condition, the model is capable of
400 addressing the extent to which phenotypic plasticity accounts for increased yearling prevalence
401 between historic and present-day reaches, but the model could be developed further to investigate
402 the role of genetically based evolution in this life history shift (e.g., by adding heritable variation
403 in thresholds or growth rates).

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418 **References**

- 419 Alderdice, D., and F. Velsen. 1978. Relation between temperature and incubation time for eggs of
420 Chinook salmon (*Oncorhynchus tshawytscha*). Journal of the Fisheries Research Board of
421 Canada 35:69–75.
- 422 Angilletta, M., E. Steel, K. Bartz, J. Kingsolver, M. Scheuerell, B. Beckman, and L. Crozier. 2008.
423 Big dams and salmon evolution: changes in thermal regimes and their potential evolutionary
424 consequences. Evolutionary Applications 1:286–299.
- 425 Aubin-Horth, N., J. Bourque, G. Daigle, R. Hedger, and J. Dodson. 2006. Longitudinal gradients
426 in threshold sizes for alternative male life history tactics in a population of Atlantic salmon
427 *salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences 63:2067–2075.
- 428 Aubin-Horth, N., and J. Dodson. 2004. Influence of individual body size and variable thresholds
429 on the incidence of a sneaker male reproductive tactic in Atlantic salmon. Evolution 58:136–144.
- 430 Beacham, T., and C. Murray. 1989. Variation in developmental biology of sockeye salmon
431 (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*) in British Columbia. Canadian
432 Journal of Zoology 67:2081–2089.
- 433 Beckman, B., B. Gadberry, P. Parkins, K. Cooper, and K. Arkush. 2007. State-dependent life
434 history plasticity in Sacramento River winter-run Chinook salmon (*Oncorhynchus tshawytscha*):
435 interactions among photoperiod and growth modulate smolting and early male maturation.
436 Canadian Journal of Fisheries and Aquatic Sciences 64:256–271.
- 437 Bradford, M. 1995. Comparative review of Pacific salmon survival rates. Canadian Journal of
438 Fisheries and Aquatic Sciences 52:1327–1338.
- 439 Brannon, E., M. Powell, T. Quinn, and A. Talbot. 2004. Population structure of Columbia River
440 Basin Chinook salmon and steelhead trout. Reviews in Fisheries Science 12:99–232.
- 441 Buchanan, R., J. Skalski, and G. McMichael. 2009. Differentiating mortality from delayed
442 migration in subyearling fall Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of
443 Fisheries and Aquatic Sciences 66:2243–2255.

444 Carlson, S., and T. Seamons. 2008. A review of quantitative genetic components of fitness in
445 salmonids: implications for adaptation to future change. *Evolutionary Applications* 1:222–238.

446 Clarke, W., and J. Blackburn. 1977. A seawater challenge test to emasure smolting in juvenile
447 salmon. Canada Department of the Environment, Fisheries and Marine Service, Research and
448 Development Directorate. Technical Report 705:1–11.

449 Clarke, W., R. Withler, and J. Shelbourn. 1994. Inheritance of smolting phenotypes in backcrosses
450 of hybrid stream-type x ocean-type chinook salmon (*Oncorhynchus tshawytscha*). *Estuaries*
451 17:13–25.

452 Combs, B., and R. Burrows. 1957. Threshold temperatures for the normal development of
453 Chinook salmon eggs. *Progressive Fish Culturist* 19:3–6.

454 Connor, W., and H. Burge. 2003. Growth of wild subyearling fall Chinook salmon in the Snake
455 River. *North American Journal of Fisheries Management* 23:594–599.

456 Connor, W., H. Burge, R. Waitt, and T. Bjornn. 2002. Juvenile life history of wild fall Chinook
457 salmon in the Snake and Clearwater Rivers. *North American Journal of Fisheries Management*
458 22:703–712.

459 Connor, W., S. Smith, T. Andersen, S. Bradbury, D. Burum, E. Hockersmith, M. Schuck,
460 G. Mendel, and R. Bugert. 2004. Postrelease performance of hatchery yearling and subyearling
461 fall Chinook salmon released into the Snake River. *North American Journal of Fisheries*
462 *Management* 24:545–560.

463 Connor, W., J. Sneva, K. Tiffan, R. Steinhorst, and D. Ross. 2005. Two alternative juvenile life
464 history types for fall Chinook salmon in the Snake River basin. *Transactions of the American*
465 *Fisheries Society* 134:291–304.

466 Connor, W., R. Steinhorst, and H. Burge. 2000. Forecasting survival and passage of migratory
467 juvenile salmonids. *North American Journal of Fisheries Management* 20:651–660.

468 ———. 2003. Migrational behaviour and seaward movement of wild subyearling fall Chinook
469 salmon in the Snake River. *North American Journal of Fisheries Management* 23:414–430.

- 470 Crozier, L., A. Hendry, P. Lawson, T. Quinn, N. Mantua, J. Battin, R. Shaw, and R. Huey. 2008.
471 Potential responses to climate change in organisms with complex life histories: evolution and
472 plasticity in Pacific salmon. *Evolutionary Applications* 1:252–270.
- 473 Curet, T. 1993. Habitat use, food habits and the influence of predation on subyearling Chinook
474 salmon in Lower Granite and Little Goose Reservoirs, Washington. M.S. thesis. University of
475 Idaho.
- 476 Garcia, A., S. Bradbury, B. Arnsberg, S. Rocklage, and P. A. Groves. 2004. Fall Chinook salmon
477 spawning ground surveys in the Snake River basin upriver of Lower Granite Dam. Tech. rep.,
478 Bonneville Power Administration, Portland, OR.
- 479 Garling, D., and M. Masterson. 1985. Survival of Lake Michigan Chinook salmon eggs and fry
480 incubated at three temperatures. *Progressive Fish Culturist* 47:63–66.
- 481 Geist, D. R., C. S. Abernethy, K. D. Hand, V. I. Cullinan, J. A. Chandler, and P. A. Groves. 2006.
482 Survival, development, and growth of fall Chinook salmon embryos, alevins, and fry exposed to
483 variable thermal and dissolved oxygen regimes. *Transactions of the American Fisheries Society*
484 135:1462–1477.
- 485 Groot, G., and L. Margolis, eds. 1991. *Pacific Salmon Life Histories*. UBC Press.
- 486 Groves, P., J. Chandler, and T. Richter. 2008. Comparison of temperature data collected from
487 artificial Chinook salmon redds and surface water in the Snake River. *North American Journal*
488 *of Fisheries Management* 28:766–780.
- 489 Hazel, W., R. Smock, and M. Johnson. 1990. A polygenic model for the evolution and
490 maintenance of conditional strategies. *Proceedings of the Royal Society B* 242:181–187.
- 491 Hazel, W., R. Smock, and C. Lively. 2004. The ecological genetics of conditional strategies.
492 *American Naturalist* 163:888–900.
- 493 Heming, T. 1982. Effects of temperature on utilization of yolk by Chinook salmon (*Oncorhynchus*
494 *tshawytscha*) eggs and alevins. *Canadian Journal of Fisheries and Aquatic Sciences* 39:184–190.

495 Hoar, W. 1976. Smolt transformation: Evolution, behavior, and physiology. *Journal of the*
496 *Fisheries Research Board of Canada* 33:1233–1252.

497 Jensen, J., and E. Groot. 1991. The effect of moist air incubation conditions and temperature on
498 Chinook salmon egg survival. *American Fisheries Society Symposium* 10:529–538.

499 Koseki, Y., and I. Fleming. 2006. Spatio-temporal dynamics of alternative male phenotypes in
500 coho salmon populations in response to ocean environment. *Journal of Animal Ecology*
501 75:445–455.

502 ———. 2007. Large-scale frequency dynamics of alternative male phenotypes in natural
503 populations of coho salmon (*Oncorhynchus kisutch*): patterns, processes, and implications.
504 *Canadian Journal of Fisheries and Aquatic Sciences* 64:743–753.

505 Koski, K. 2009. The fate of coho salmon nomads: The story of an estuarine-rearing strategy
506 promoting resilience. *Ecology and Society* 14:4.

507 McMichael, G., C. Rakowski, B. James, and J. Lukas. 2005. Estimated fall Chinook salmon
508 survival to emergence in dewatered redds in a shallow side channel of the Columbia River.
509 *North American Journal of Fisheries Management* 25:876–884.

510 Milks, D., M. Varney, and M. Schuck. 2009. Lyons Ferry Hatchery Evaluation, Fall Chinook
511 Salmon, Annual Report: 2006. Tech. rep., Washington Department of Fish and Wildlife, Fish
512 Program, Science Division.

513 Muir, W., S. Smith, E. Hockersmith, M. Eppard, W. Connor, T. Andersen, and B. Arnsberg.
514 1999. Fall chinook salmon survival and supplementation studies in the snake river and lower
515 snake river reservoirs, 1997. Annual report (DOE/BP-10891-8) to Bonneville Power
516 Administration, Portland, OR, Contracts DE-AI79-93BP10891 and DE-AI79-91BP21708,
517 Projects 93-029-00 and 91-029-00, 71 p. (BPA Report DOE/BP-10891-8) .

518 Murray, C., and J. McPhail. 1988. Effect of incubation temperature on the development of five
519 species of Pacific salmon (*Oncorhynchus*) embryos and alevins. *Canadian Journal of Zoology*
520 66:266–273.

521 Myers, R., J. Hutchings, and R. Gibson. 1986. Variation in male parr maturation within and
522 among populations of Atlantic salmon, *salmo salar*. Canadian Journal of Fisheries and Aquatic
523 Sciences 43:1242–1248.

524 Narum, S., J. Stephenson, and M. Campbell. 2007. Genetic variation and structure of Chinook
525 salmon life history types in the Snake River. Transactions of the American Fisheries Society
526 136:1252–1262.

527 National Marine Fisheries Service. 1995. Endangered and threatened species; status of Snake
528 River spring/summer chinook salmon and Snake River fall chinook salmon. Final Rule. Federal
529 Register [Docket No. 950412102-5102-01; I.D. 072594B] 60:19341–19342.

530 R Development Core Team. 2009. R: A Language and Environment for Statistical Computing. R
531 Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

532 Rikardsen, A., J. Thorpe, and J. Dempson. 2004. Modelling the life-history variation of Arctic
533 charr. Ecology of Freshwater Fish 13:305–311.

534 Satterthwaite, W. H., M. Beakes, E. Collins, D. Swank, J. Merz, R. Titus, S. Sogard, and
535 M. Mangel. 2009a. State-dependent life history models in a changing (and regulated)
536 environment: steelhead in the california central valley. Evolutionary Applications .

537 ———. 2009b. Steelhead life history on California’s central coast: Insights from a state-dependent
538 model. Transactions of the American Fisheries Society 138:532–548.

539 Smith, S., W. Muir, E. Hockersmith, R. Zabel, R. Graves, C. Ross, W. Connor, and B. Arnsberg.
540 2003. Influence of river conditions on survival and travel time of Snake River subyearling fall
541 Chinook salmon. North American Journal of Fisheries Management 23:939–961.

542 Sykes, G., C. Johnson, and J. Shrimpton. 2009. Temperature and flow effects on migration timing
543 of Chinook salmon smolts. Transactions of the American Fisheries Society 138:1252–1265.

544 Theriault, V., D. Garant, L. Bernatchez, and J. Dodson. 2007. Heritability of life-history tactics
545 and genetic correlation with body size in a natural population of brook charr (*Salvelinus*
546 *fontinalis*). Journal of Evolutionary Biology 20:2266–2277.

547 Thorpe, J., M. Mangel, N. Metcalfe, and F. Huntingford. 1998. Modelling the proximate basis of
548 salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L.
549 Evolutionary Ecology 12:581–599.

550 Tomkins, J., and W. Hazel. 2007. The status of the conditional evolutionarily stable strategy.
551 Trends in Ecology and Evolution 22:522–528.

552 Unwin, M., T. Quinn, M. Kinnison, and N. Boustead. 2000. Divergence in juvenile growth and life
553 history in two recently colonized and partially isolated chinook salmon populations. Journal of
554 Fish Biology 57:943–960.

555 Waples, R., G. Pess, and T. Beechie. 2008*a*. Evolutionary history of Pacific salmon in dynamic
556 environments. Evolutionary Applications 1:189–206.

557 Waples, R., R. Zabel, M. Scheuerell, and B. Sanderson. 2008*b*. Evolutionary responses by native
558 species to major anthropogenic changes to their ecosystems: Pacific salmon in the Columbia
559 River hydropower system. Molecular Ecology 17:84–96.

560 Wedemeyer, G., R. Saunders, and W. Clarke. 1980. Environmental factors affecting smoltification
561 and early marine survival of anadromous salmonids. Marine Fisheries Review 42:1–14.

562 Williams, J., R. Zabel, R. Waples, J. Hutchings, and W. Connor. 2008. Potential for
563 anthropogenic disturbances to influence evolutionary change in the life history of a threatened
564 salmonid. Evolutionary Applications 1:271–285.

565 Zaugg, W., and L. McLain. 1976. Influence of water temperature on gill sodium,
566 potassium-stimulated atpase activity in juvenile coho salmon (*Oncorhynchus kisutch*).
567 Comparative Biochemistry and Physiology 54A:419–421.

568 **Appendix**

569 *Daily Fry Survival Parameter Estimation*

570 In the empirical study (Connor et al. 2004) from which these estimates are derived, the
571 authors PIT-tagged a number of fish, released them at Pittsburg Landing in the upper Snake
572 River, and recaptured the emigrating survivors at Lower Granite Dam. Prior to release, fish were
573 reared under one of four treatments at Lyons Ferry Hatchery and constituted a range of sizes at
574 the time of release. This procedure was conducted in two years (1997 and 1998), yielding a total
575 of eight observations (four rearing groups \times two years). Data for these eight groups are
576 well-explained by simple functions of length at release, including mean time between release and
577 recapture = $e^{11.93} \times \text{release length}^{-1.88}$ ($R^2 = 0.92$), mean growth rate during the release period =
578 $0.025 - 0.00015 \times \text{release length}$ ($R^2 = 0.93$), and survival during the release period =
579 $0.891 / (1 + \exp((73.6 - \text{release length})/11.3))$ ($R^2 = 0.91$).

580 Because the empirical study did not take into account that a proportion of the PIT-tagged fish
581 over-wintered above Lower Granite Dam instead of migrating as subyearlings, the survival
582 quantity that Connor et al. (2004) report is actually the joint probability of surviving and
583 migrating. To account for the influence of migration in these survival estimates, we divided the
584 joint probability of surviving and migrating by the probability of migrating (i.e., the subyearling
585 proportion from Connor et al. 2002) and thereby obtained an estimate of the probability of
586 surviving. Although to our knowledge the same individuals were not used in the two studies (i.e.,
587 Connor et al. 2002, 2004), the studies are compatible because both involved PIT-tagging fish of
588 similar sizes and releasing them on similar dates from the upper Snake River in 1997 and 1998.
589 The probabilities of migrating in the years in which survival estimates were made were 1 and
590 0.981, and the probability of migrating was no less than 0.957 in any other year in which
591 migration probabilities were reported. Therefore, we conclude that a majority ($\sim 99\%$) of upper
592 Snake River fish in these years adopted a subyearling life history and migrated, meaning that the
593 joint probability of surviving and migrating from Connor et al. (2004) is approximately equal to
594 the probability of surviving. Because the difference between the joint probability of surviving and
595 migrating and the probability of surviving are so similar, we used the survival estimates from
596 Connor et al. (2004) without modification.

597 The study of Connor et al. (2004) only applies directly to fish ≥ 70.8 mm, but daily survival
 598 estimates are needed for fry as small as 30.7 mm in our model. We therefore made adjustments to
 599 extrapolate the curves fit in the empirical study to this smaller size. To extend the curve for time
 600 between release and recapture, we first assumed that fry do not begin active migration
 601 immediately following emergence. We then assumed that the mean time between release of newly
 602 emerged fry and their recapture at lower Granite Dam should account for both the initial growth
 603 period (at rate $1.1 \text{ mm}\cdot\text{d}^{-1}$, Connor and Burge 2003) and observed migration time such that this
 604 quantity = $(70.8 - \text{release length})/1.1 + e^{11.93} \times \text{release length}^{-1.88}$ for $30.7 \leq \text{release length}$
 605 ≤ 70.8 . To extend the curve for survival during the release period, we added an extra datum
 606 representing the survival (0.1515) of newly emerged fry (30.7 mm) until the time at which they
 607 begin active migration toward Lower Granite Dam. This quantity was obtained by dividing the
 608 expected survival between egg deposition and outmigration for fall Chinook salmon (0.086)
 609 (Bradford 1995) into the average simulated survival between egg deposition and emergence in our
 610 model (0.8437) and the midpoint of the range of survivals during the release period (0.673)
 611 (Connor et al. 2004). With the addition of this datum, the revised best-fit curve for cumulative
 612 survival during the release period is $0.1446 + (0.8881 - 0.1446) / (1 + \exp((77.45 - \text{release length})$
 613 $/ 9.969))$ ($R^2 = 0.9569$).

614 Despite a wealth of information about the release period as a whole, no data exist on daily
 615 growth or survival. We assumed constant daily growth of $1.1 \text{ mm}\cdot\text{d}^{-1}$, regardless of size, which is
 616 consistent with observed fry growth in the Snake River (Connor and Burge 2003) and the
 617 observation that percent-length growth rate decreases as fry grow (Connor et al. 2004). To derive
 618 an estimate of daily fry survival, we first wrote cumulative survival during the release period as

$$S_T(l_0) = \prod_{t=0}^{T(l_0)-1} s(l_t(l_0)) ,$$

619 where l_T is length on day t , T is the mean time between release and recapture, and $s(l_t)$ is a
 620 proposed model for daily growth. Applying the ‘optim’ function in R (R Development Core Team
 621 2009) for optimization, we then found that the survival model that maximized R^2 between $S_T(l_0)$
 622 and the fitted curve for survival during the release period is the function in Eqn. (2)
 623 ($R^2 = 0.9819$). To ensure that the assumption that survival over the duration of residence in the

624 natal stream is approximated by the survival estimates of Connor et al. (2004) had no significant
625 impact on our estimates of daily fry survival, we repeated the daily fry survival parameter fitting
626 procedure with survival probabilities that took into account the probability of migrating. Doing so
627 showed that accounting for the probability of migrating had no impact on daily survival
628 parameters to a precision of at most the third significant digit. There was also no effect on best-fit
629 threshold parameter values reported in the main text.

630 TABLES

631 Table 1. Regression relationships used to impute water temperature at one gage based on
 632 measurements at another. Gage abbreviations are GR = Grande Ronde R.; PK = Fort Peck,
 633 Clearwater R.; SP = Spalding, Clearwater R.; LS and US = lower and upper Snake R.

Gage	Primary			Secondary		
	Regression	Adj. R ²	RMSE	Regression	Adj. R ²	RMSE
GR	-2.73+1.08 LS	0.89	2.37	-2.95+1.54 SP	0.81	3.11
634 PK	0.26+0.89 SP	0.96	0.70	1.19+0.55 LS	0.83	1.57
LS	-0.96 + 1.01 US	0.96	1.23	3.45 + 0.82 GR	0.89	2.06
SP	-0.02+1.08 PK	0.97	0.77	1.19+0.61 LS	0.82	1.77
US	1.38 + 0.95 LS	0.97	1.20	5.06 + 0.74 GR	0.77	2.93

635 Table 2. Best-fit thresholds under different assumptions about accumulated thermal unit (ATU)
636 threshold for emergence, fork length (FL) at emergence, and whether there is individual variation
637 in those parameters. Due to higher computational demands, $D^* = 253$ was used in simulations
638 with variation in emergence ATU and FL to constrain the best-fit parameter search to a single
639 day-of-year (DOY) threshold that is never attained.

		Variation in emergence ATU and FL							
		No				Yes			
		944 ATU		1066 ATU		944 ATU		1066 ATU	
640		30.7 mm	35.2 mm	30.7 mm	35.2 mm	30.7 mm	35.2 mm	30.7 mm	35.2 mm
D^*		169	167	211	177	–	–	–	–
L^*		41	46	35	40	45	48	35	40
T^*		14	14	14	14	14	14	14	14

641 Table 3. Simulated and empirical yearling percentages by river and year. Simulated percentages
 642 were obtained by simulating the model with best-fit threshold values. Empirical percentages are
 643 those reported by Connor et al. (2002).

Year	Upper Snake		Lower Snake		Clearwater	
	Simulated	Empirical	Simulated	Empirical	Simulated	Empirical
1991			5.5	4.4		
1992			0.2	15.7	55.0	67.1
1993			53.1	24.6	75.6	84.6
644 1994	3.4	0.9	13.3	3.8	25.2	6.3
1995	0.0	3.3	0.0	4.7		
1996	2.9	0.0	0.0	18.5		
1997	4.8	1.9	0.0	3.9		
1999	2.2	4.3	0.0	13.9		

645 Table 4. Mean \pm SE of simulated and empirical yearling percentages across years. Data used to
646 calculate mean percentages in 1991-1999 are taken from years in which Connor et al. (2002) report
647 observations: 1994-1997, 1999 for upper Snake; 1991-1997, 1999 for lower Snake; 1992-1994 for
648 Clearwater. Simulated percentages were obtained by simulating the model with best-fit threshold
649 values. Empirical percentages for 1991-1999 are those reported by Connor et al. (2002), whereas
650 those from 2000-2005 come from unpublished data from W.P. Connor that he collected in the
651 same way.

Years	Upper Snake		Lower Snake		Clearwater	
	Simulated	Empirical	Simulated	Empirical	Simulated	Empirical
1991-1999	2.7 \pm 0.8	2.1 \pm 0.8	9.0 \pm 6.5	11.2 \pm 2.9	51.9 \pm 14.6	52.7 \pm 23.7
2000-2005	11.5 \pm 20.8	1.9 \pm 1.1	11.7 \pm 21.4	3.1 \pm 1.2		

653 **FIGURE LEGENDS**

654 Figure 1. Map of the Snake River spawning area for fall Chinook salmon and its surroundings.

655 Bars across rivers represent dams, and crosshatched ellipses are distinct spawning areas.

656 Numbered locations are as follows: 1 = Hells Canyon Dam; 2 = upper reach of the Snake River; 3

657 = lower reach of the Snake River; 4 = lower reach of the Clearwater River; 5 = Dworshak Dam; 6

658 = Lower Granite Reservoir; 7 = Lower Granite Dam. Map was taken from Figure 1 of Connor

659 et al. (2002) and modified.

660 Figure 2. Schematic representation of fall Chinook salmon development and its dependence on

661 temperature under model assumptions. Bold text signifies distinct life stages, regular text denotes

662 developmental transitions, and italicized text indicates criteria for those transitions. Life history

663 differentiation is triggered by whichever of the temperature or day-of-year (DOY) thresholds is

664 triggered first. Temperature data come from the upper reach of the Snake River, with the date

665 and temperature axes spanning ranges of November 6, 1996–November 5, 1997 and -5 – 29° C.

666 Figure 3. Daily mean water temperature and yearling proportions for years in which empirical

667 yearling proportions are available. Similar to Figure 2, dots on each panel's horizontal axis from

668 left to right signify the days on which spawning, hatching, emergence, and life-history

669 differentiation occur. Indicated spawning dates are mean values, which differ among reaches. Gray

670 lines in each panel mark best-fit day-of-year (vertical) and temperature (horizontal) thresholds.

671 Corresponding to each temperature panel, pie graphs show the simulated (upper) and empirical

672 (lower) proportions of subyearlings (gray) and yearlings (black).

673 Figure 4. Sum of squares profiles for best-fit day-of-year (a), length (b), and temperature (c)

674 threshold parameters. As the focal parameter in each panel is varied, the other two threshold

675 parameters are held constant at their best-fit values. Quantitatively, $SSQ = 0$ implies a perfect

676 correspondence between simulated and empirical yearling proportions, $SSQ = 1.31$ when all

677 simulated juveniles become subyearlings, $SSQ = 12.61$ when all simulated juveniles become

678 yearlings, and $0 < SSQ < 12.61$ when simulated juveniles are a mixture of life histories. The best-fit

679 value of the focal parameter in each panel is denoted with an arrow ($SSQ = 0.2341$).

680 Figure 5. Sum of squares contour plot for length and temperature threshold parameters, with the
681 day-of-year threshold parameter held constant at a value of $D = 253$ so that the day-of-year
682 threshold is never triggered. Contours occur at intervals of 1 between 1 and 12, and shaded areas
683 accentuate parameter regions with the lowest sums of squares. Quantitatively, $SSQ = 0$ implies a
684 perfect correspondence between simulated and empirical yearling proportions, $SSQ = 1.31$ when
685 all simulated juveniles become subyearlings, $SSQ = 12.61$ when all simulated juveniles become
686 yearlings, and $0 < SSQ < 12.61$ when simulated juveniles are a mixture of life histories. Different
687 panels reflect SSQ between simulated results and those applying Eqn. (3) and different values of
688 over-winter survival u to the empirical results from Connor et al. (2002): $u = 1.0$ (a), $u = 0.75$ (b),
689 $u = 0.5$ (c), $u = 0.25$ (d).

690 Figure 6. Discrepancy between empirical estimates of the proportion of yearling migrants (shown
691 by dots) and the proportion of juveniles that exhibit yearling behavior in the first place as a
692 function of over-winter survival u . If $u \approx 1$, then the proportion of yearling migrants reflects the
693 proportion of juveniles that adopted a yearling life history in the first place. If $u < 1$, then the
694 proportion of yearlings is greater at the time of life-history differentiation than it is at migration.
695 Curves come from Eqn. (3), with p equal to empirical estimates of the proportion of yearling
696 migrants (Connor et al. 2002).

697 Figure 7. Fork length distribution at the time of life-history differentiation and yearling
698 proportions for years in which empirical yearling proportions are available. Bars represent bins
699 2.5 mm wide ranging 36-120 mm, and fish falling in the leftmost bin include alevins that have not
700 yet emerged from the gravel but later become yearlings. Bars to the left of the best-fit length
701 threshold of $L^* = 40$ mm represent subyearlings (gray) and bars to the right represent yearlings
702 (black). Pie graphs show the simulated (upper) and empirical (lower) proportions of subyearlings
703 (gray) and yearlings (black).

Figure 1.

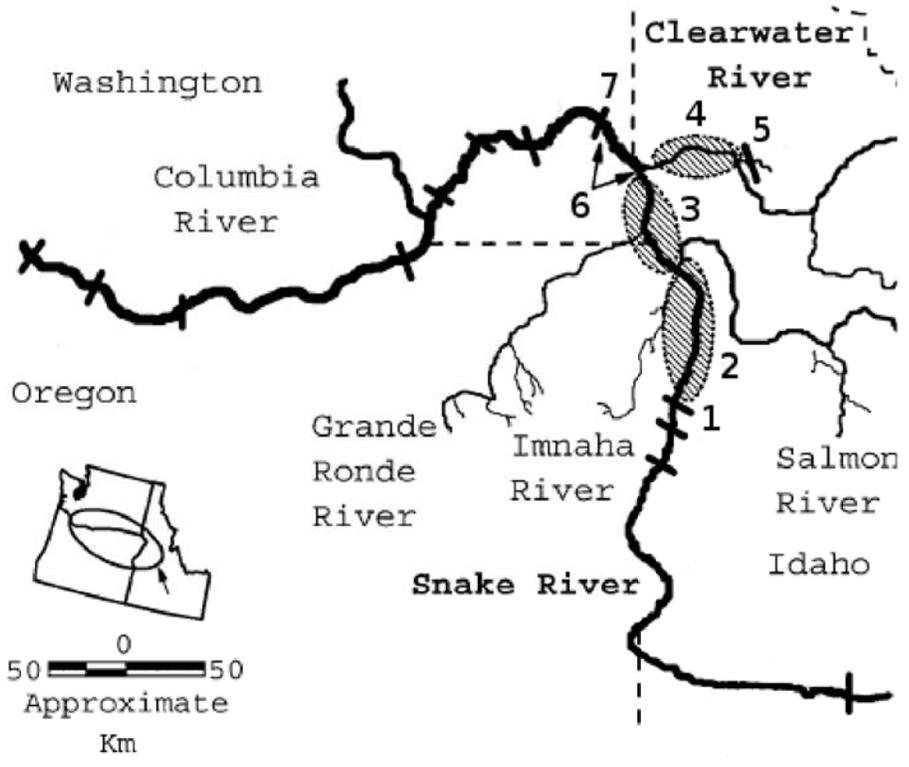


Figure 2.

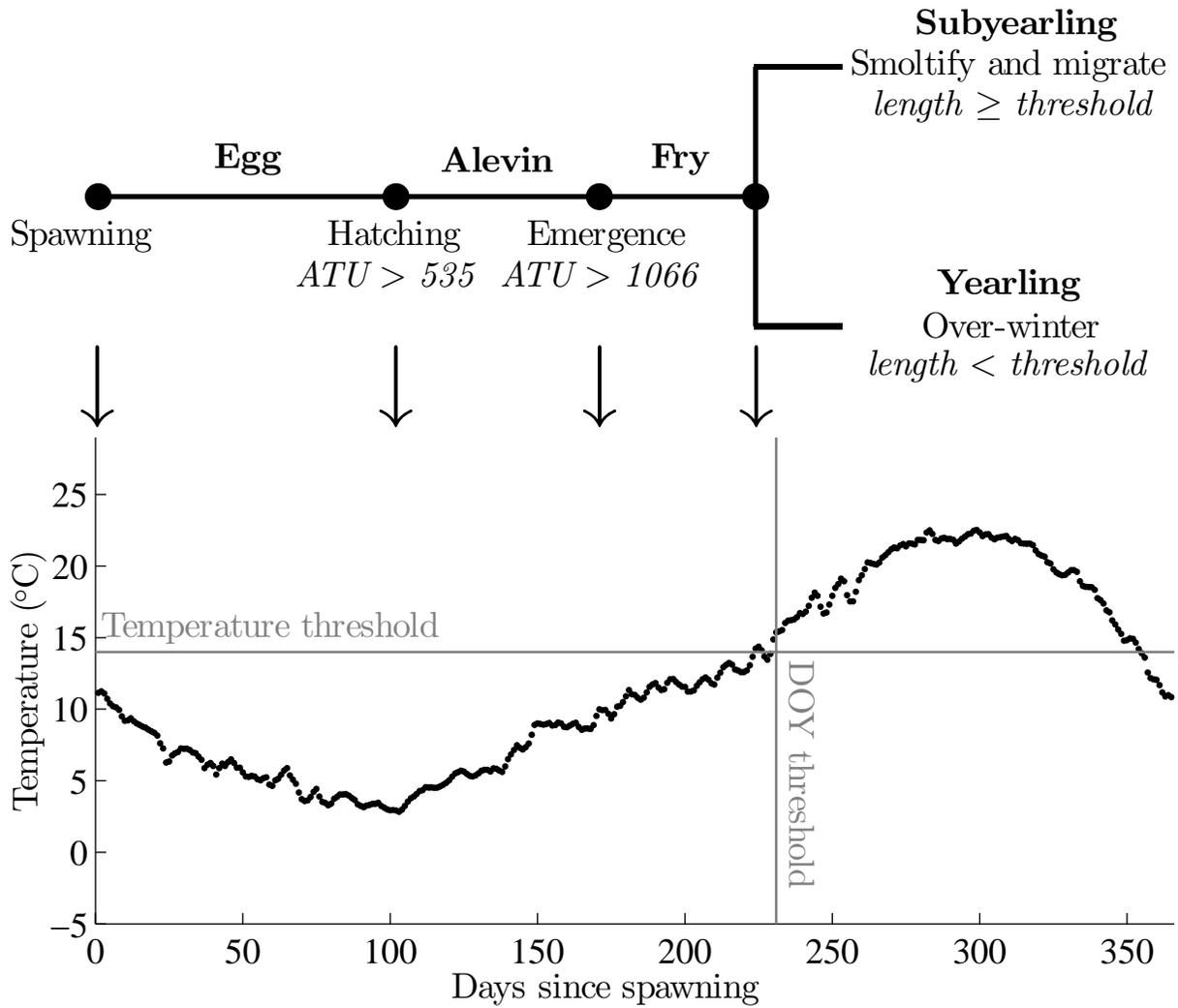


Figure 3.

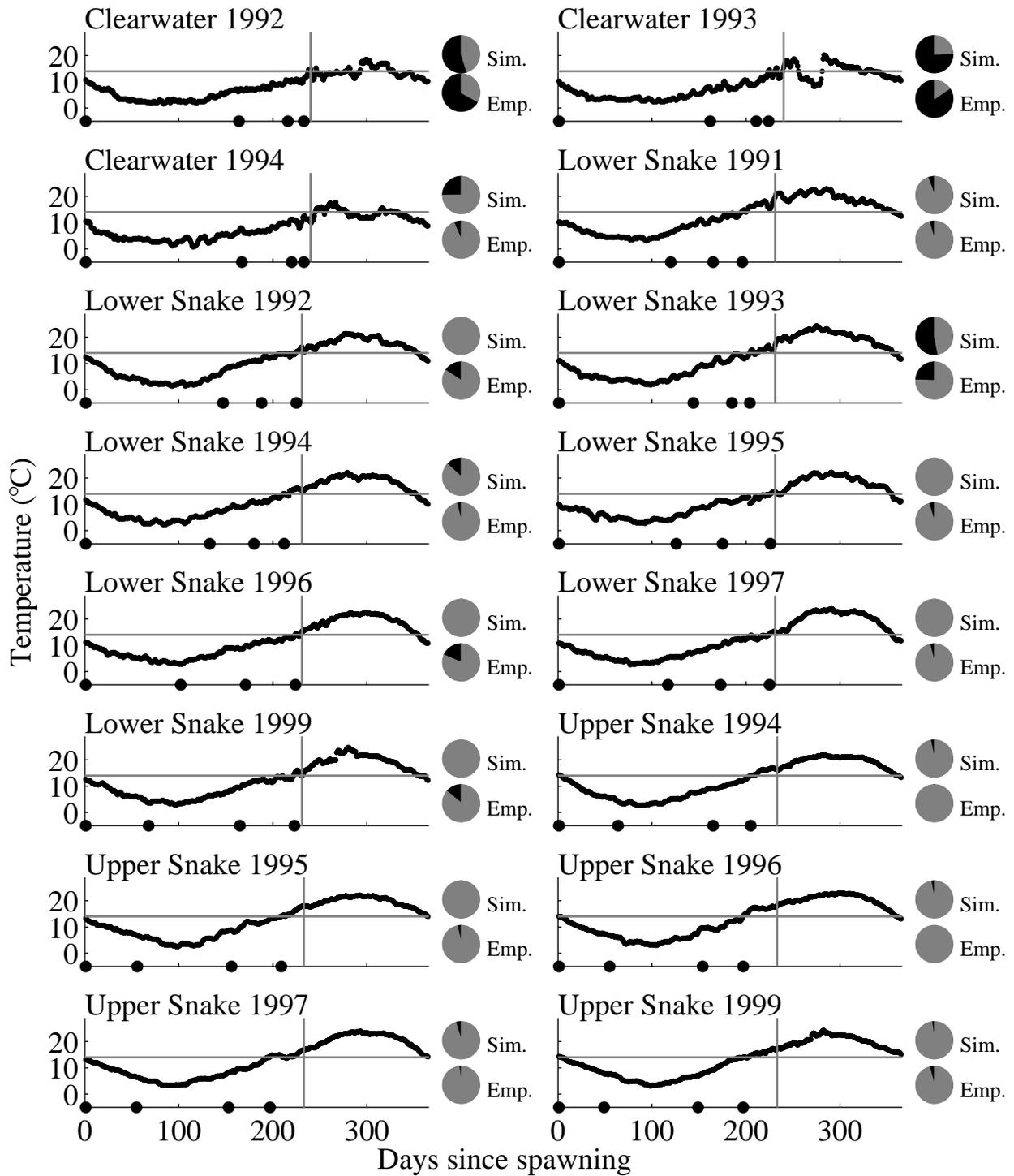


Figure 4.

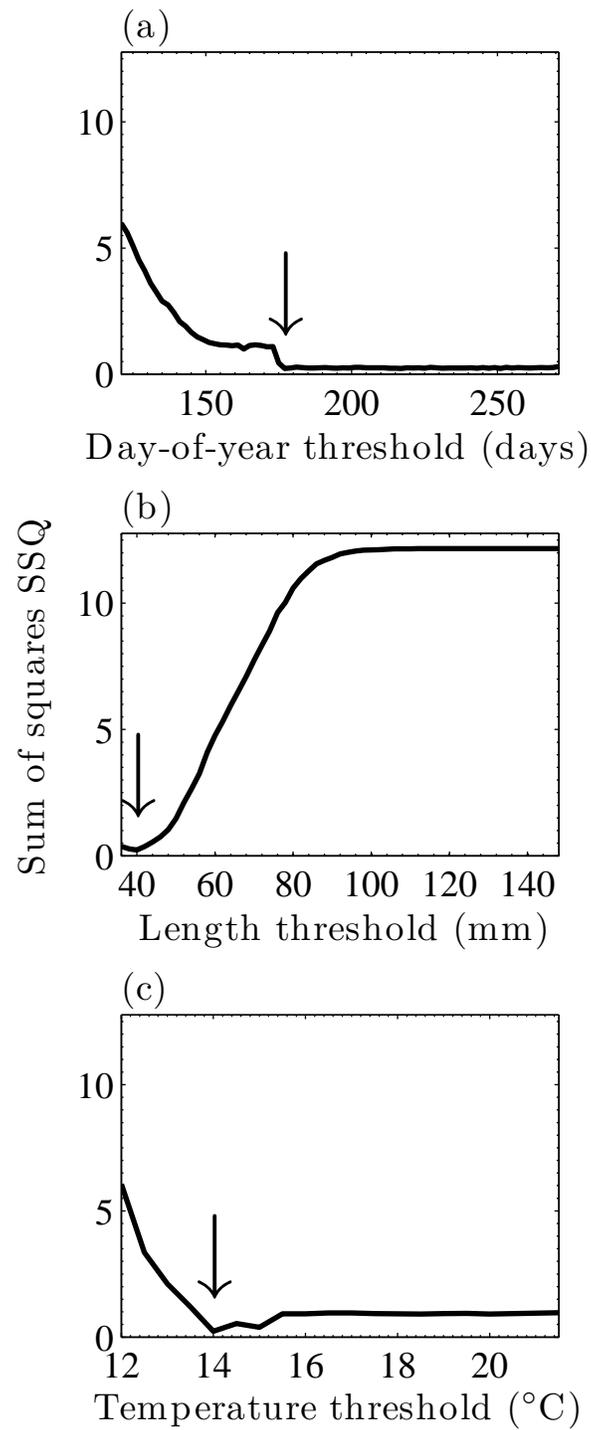


Figure 5.

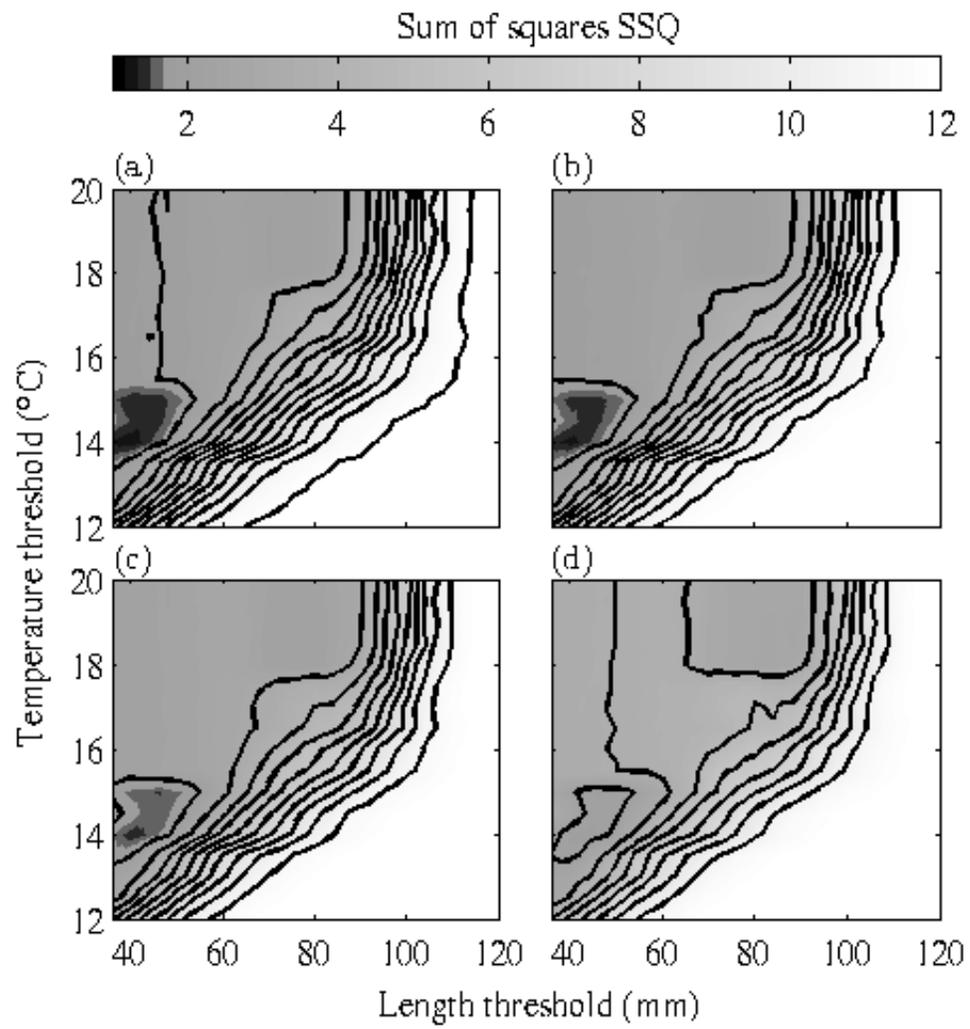


Figure 6.

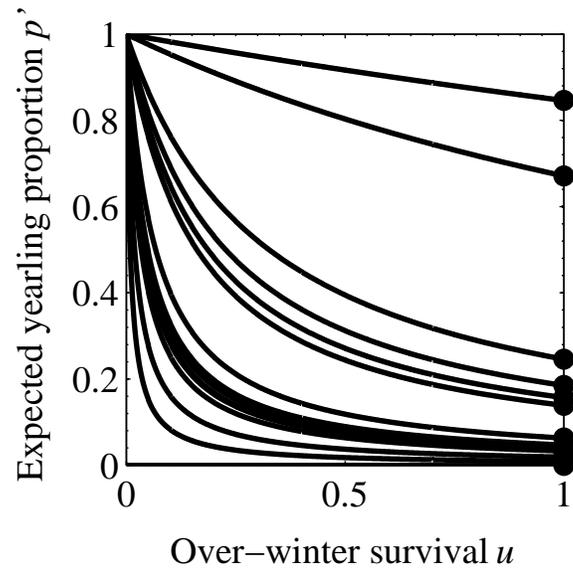


Figure 7.

