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Prepared By: Donna Parrish

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2 Running head: **Dams as migration barriers**

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4 **Migration delays caused by anthropogenic barriers: modeling dams, temperature,**  
5 **and success of migrating salmon smolts**

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7 Elizabeth A. Marschall<sup>1</sup>  
8 The Ohio State University

9

10 Martha E. Mather<sup>2</sup>  
11 U. S. Geological Survey, Massachusetts Cooperative Fish and Wildlife Research Unit

12

13 Donna L. Parrish<sup>3</sup>  
14 U. S. Geological Survey, Vermont Cooperative Fish and Wildlife Research Unit

15

16 Gary W. Allison<sup>4</sup>  
17 The Ohio State University

18

19 James R. McMenemy<sup>5</sup>  
20 Vermont Fish and Wildlife Department

21

22

23

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<sup>1</sup> marschall.2@osu.edu

<sup>2</sup> mather@nrc.umass.edu

<sup>3</sup> Donna.Parrish@uvm.edu

<sup>4</sup> allison.100@osu.edu

<sup>5</sup> Jay.McMenemy@state.vt.us

25 *Abstract.* Conservation and restoration of animal populations in the face of disruptions to  
26 migrations is a growing problem. Anthropogenic barriers along migration paths can  
27 delay migrations or increase their duration, which may result in a mismatch with  
28 migration timing adaptations. To understand the interaction of dams (as barriers along a  
29 migration path), seasonally changing environmental conditions, timing of Atlantic  
30 salmon (*Salmo salar*) downstream migration, and ultimate migration success, we used ten  
31 years of river temperature and discharge data as a template upon which we simulated  
32 downstream movement of salmon. Atlantic salmon is a coolwater species whose  
33 downstream migrating smolts must complete migration before river temperatures become  
34 too warm. We found that dams had a local effect on survival as well as a survival effect  
35 that was spatially and temporally removed from the encounter with the dam. By delaying  
36 smolts until temperatures downstream had reached lethal or near-lethal temperatures,  
37 dams served to disrupt the match between completion of migration and the window of  
38 appropriate migration conditions. Our simulations show that the strength of this spatially  
39 and temporally removed effect is at least comparable to the local effects of dams in  
40 determining smolt migration success in the presence of dams. We also considered smolts  
41 from different tributaries, varying in distance from the river mouth, to assess the potential  
42 importance of locally adapted migration timing on the effect of barriers. Our results  
43 demonstrate that migration-initiation temperature affected modeled smolt survival  
44 differentially across tributaries, with the success of smolts from upstream tributaries  
45 being much more variable across years than that of smolts with a shorter distance to  
46 travel. As a whole, these results point to the importance of broadening our spatial and  
47 temporal view when managing migrating populations. We must consider not only how

48 many individuals never make it across migration barriers, but also the spatially and  
49 temporally removed consequences of delays at the barriers for those individuals that  
50 successfully navigate them.

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52 *Keywords: migration; migration barriers; migration delay; Atlantic salmon; dams;*  
53 *smolts; movement barriers.*

54

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## INTRODUCTION

56 Anthropogenic barriers along migration paths can completely block migration  
57 routes (Ito et al. 2005; Epps et al. 2007; Wilcove and Wikelski 2008) or can delay  
58 migration (Brown et al 2003; Acou et al. 2008), disrupting evolutionarily selected timing  
59 of arrival at migration destinations. Changes in environmental conditions along  
60 migration routes, as a result of changes in climate (Musiega et al. 2006; Wilcove and  
61 Wikelski 2008) and land use, are further eroding the effectiveness of migration-related  
62 adaptations (Dolman and Sutherland 1995; Callaghan et al. 2004; Crozier et al. 2008).  
63 The interaction among migration barriers, disruptions of local adaptations, and changing  
64 environmental cues and conditions represents a problem for species conservation and  
65 restoration (Wilcove and Wikelski 2008).

66 Anadromous fish present an appropriate model with which to study this  
67 interaction. Altered discharge because of water withdrawals and changes in land use,  
68 increased temperatures related to climate change, and fragmentation and delays caused by  
69 dams can upset both the effectiveness of evolved cues to migration timing as well as  
70 successful completion of migration. While the effect of migration barriers has been well

71 studied in the upstream-migration phase of anadromous fish life cycles (e.g., Moser et al.  
72 2002; Caudill et al. 2007; Lundqvist et al. 2008), their effect in the downstream-migration  
73 phase has received focused attention in only a few specific systems (e.g., salmon in the  
74 Pacific northwest: Welch et al. 2008).

75         Salmonidae, a widely distributed, anadromous family with locally adapted stocks,  
76 embody several key characteristics that make them well suited to inform this problem.  
77 When a parr (juvenile freshwater life stage) transforms into a smolt (juvenile transition  
78 between fresh and salt water life stages), a complex suite of changes in body  
79 morphometry, behavior, and physiology occurs (Thorpe and Morgan 1978; McCormick  
80 et al. 1998) such that smolts are physiologically able to survive the migration and  
81 transition to seawater as they move downstream. In adapted populations, these changes  
82 and the initiation of downstream migration are cued by environmental conditions,  
83 resulting in a high likelihood of a match between timing of smolt arrival at the marine  
84 system and timing of appropriate conditions for survival. Cues for timing of migration  
85 can differ across populations. For example, Atlantic salmon (*Salmo salar*) smolts from an  
86 upper tributary begin migration earlier than those from a lower tributary (River Tay,  
87 Scotland; Stewart et al. 2006), allowing them to arrive at their destination at similar  
88 times. The timing of the suite of physiological and behavioral changes associated with  
89 the smolt stage produces a “window” of smolt readiness (McCormick et al. 1998). A  
90 successful transition from freshwater to seawater depends on the coupling of  
91 physiological readiness, ecological constraints (e.g., predators), and environmental  
92 conditions (e.g., temperature, discharge, salinity) (McCormick et al. 1998).

93           To help understand consequences of anthropogenic impediments to migration on  
94 the migration success of smolts in large rivers, we focused on the Atlantic salmon. The  
95 Atlantic salmon is critical for the function of stream and river ecosystems and has  
96 substantial value to human populations. As such, they are the object of widespread  
97 conservation and restoration efforts. Historically, Atlantic salmon populations existed in  
98 rivers as far south as Long Island Sound (USA, 41°N Lat) and the Douro River (Portugal,  
99 41° N Lat) up to arctic regions of the North Atlantic (Collette and Klein-McPhee 2002).  
100 The life cycle of Atlantic salmon varies (Marschall et al. 1998), with fish typically  
101 spending 1 to 5 years in freshwater and 1 to 3 years at sea before returning to their natal  
102 river to spawn.

103           We used a modeling approach to study the interaction between migration-timing  
104 cues, presence of dams along the migration route, distance from migratory destination,  
105 and annually varying patterns of river temperature and flow. We used temperature and  
106 discharge data from the Connecticut River as a template upon which we simulated  
107 downstream migration of smolts. While we are seeking to uncover general patterns, the  
108 interaction of flow, temperature, location on the river, season, and annual variation are  
109 too complex to represent in a simple hypothetical model. Thus, we use empirical data  
110 from the Connecticut River to provide a coarse representation of flow and temperature  
111 over the course of a large river over multiple spawning seasons. The downstream  
112 migrating smolts, however, are represented more generally as they simply respond to  
113 flow, temperature, and dams in the simulated system.

114           Smolts in this system must complete migration before downstream river  
115 temperatures become too warm (McCormick et al. 1998). While the Atlantic salmon

116 population in the Connecticut river is currently a genetic mix, resulting from a stocking  
117 program designed to restore the once extirpated population, we are interested in the  
118 general question of how local adaptations, which may have existed historically and  
119 certainly continue to exist in other systems, may play a role in the effect of migration  
120 delays. Because of their homing ability, salmon have the potential for rapid adaptation to  
121 local environmental conditions. As such, we asked about the importance of local  
122 adaptations in migration timing and the interaction between migration timing and barriers  
123 along the migration route. Our objectives were to use the model to answer the following  
124 questions: Given the present highly altered state of the flow of the river, what would be  
125 the consequence to survival of Atlantic salmon smolts migrating in response to different  
126 temperature cues, across a range of tributaries with different distances from the migration  
127 destination? How does the delay in migration associated with dams interact with  
128 temperature cues and tributary of origin to affect survival of smolts? Conservation of  
129 migrating Atlantic salmon often has been focused on management of the barrier itself.  
130 This study seeks to understand how barriers interact with potential local adaptations to  
131 drive ultimate migration success, expanding the way we consider management of the  
132 system.

## 133 METHODS

134 We simulated downstream movement of migrating Atlantic salmon smolts on a  
135 spatially and temporally explicit template of flow and temperature along the course of a  
136 long river. We simulated smolt movement out of tributaries positioned along much of the  
137 length of this river. The model of environmental conditions along the course of the  
138 Connecticut River was based on a patchwork of empirical data representing conditions

139 over a span of ten years and 428 river kilometers (RK). We suspect that the optimal time  
140 to begin downstream migration may differ according to how far from the mouth of the  
141 river a smolt begins its journey and whether it encounters delays at dams. To test the  
142 relative effect of delay at dams on smolts from different tributaries, we ran all simulations  
143 over a range of migration-initiation temperatures for eight tributaries. And because we  
144 suspect that year-to-year variability in flow and temperature conditions may give rise to  
145 annual variability in smolt downstream migration success, we included ten years of year-  
146 specific flow and temperatures.

147 *Study system*

148 The Connecticut River, the largest river in New England (660 km; 29,100 km<sup>2</sup>;  
149 Fig. 1), is an excellent watershed in which to examine interactions among anthropogenic  
150 barriers, disruption of historical local adaptation, and environmental variability in a large,  
151 altered river. The Connecticut River basin contains more than 1,000 dams basinwide  
152 (Gephard and McMenemy 2004). Our study reach extended from Wells River to the  
153 mouth, a distance of 428 km. In this reach, there are five mainstem dams (RK 349, 280,  
154 229, 192, and 138, Fig. 1), all of which have downstream fish passage facilities. Atlantic  
155 salmon were extirpated from the system in the early 1800s (Moffitt et al. 1982). A  
156 restoration program is currently underway (Meyers 1994; Connecticut River Atlantic  
157 Salmon Commission 1998) in which adults are captured upon return to the river and  
158 spawned in hatcheries, allowing up to 10 million genetically mixed juveniles (25-50 mm)  
159 to be stocked into about 38 tributary systems at known densities. After spending two  
160 winters (on average, Orciari et al. 1994; Whalen et al. 1999) in the streams, these  
161 juveniles transform into smolts and begin migrating downstream in the spring. Although

162 adult Atlantic salmon returns to the Connecticut River have been consistently low (for  
163 example, adult returns from 1995-2004 averaged 230, range = 40-300), Connecticut  
164 River Atlantic salmon are not listed as an endangered species because the native stock is  
165 extinct.

### 166 *Structure of the model*

167 We developed an individual-based model of downstream migrating smolts. We  
168 modeled the river in 1.61-km segments, with temperature and flow rate in each segment  
169 updated daily from ten years of empirical data interpolated over the entire 428-km study  
170 reach (Appendix A). For each simulation year, we simulated 500 smolts leaving each of  
171 eight tributaries to begin the migration down the Connecticut River to the mouth at Long  
172 Island Sound. We tracked the location of each simulated smolt each day; a smolt's  
173 location on a given day was determined by its location the previous day, current speed at  
174 its previous location, movement speed (a constant) in relation to current speed, and  
175 whether the smolt was delayed at a dam. Smolts experienced mortality risk due to  
176 background natural mortality, mortality directly at the dam, and mortality from extreme  
177 temperatures. In the methods below, we provide details on the structure of each piece of  
178 the model and how parameters were estimated.

### 179 *Modeling flow and temperature*

180 Our goal was to represent the large-scale spatial patterns in flow and temperature over the  
181 course of a long river and the intraseasonal and interannual variation in these large-scale  
182 patterns. Flow data, in the form of river discharge values, were obtained from the United  
183 States Geological Services (USGS) National Water Information System  
184 (<http://waterdata.usgs.gov/nwis>) and converted into current velocity (linear distance per

185 time). We used flow data from each of 10 years (1993-2002) from four sites (RK 428,  
186 346, 191, and 101) and interpolated between sites. (See Appendix A for additional  
187 details of flow data.) Upon this flow template, we added the five mainstem dams in our  
188 study area. In practice, rather than modeling a dam's effect on current velocity, we  
189 modeled its effect on smolt movement rates relative to the background flow of the river  
190 (see "Delay at Dams" below). We were interested in understanding dams as barriers to  
191 smolt movement rather than understanding how dams affect flow and temperature  
192 dynamics of the river.

193 To model temperature, we used mean daily temperature data from eight sites  
194 along the course of the river (RK 605, 554, 272, 192, 138, 101, 21, and 0). Temperature  
195 data were supplied by USGS National Water Information System, Vermont Agency of  
196 Natural Resources, Massachusetts Division of Fisheries and Wildlife, NOAA, and  
197 Connecticut Yankee Nuclear Power Plant (currently decommissioned). (See Appendix A  
198 for additional details of temperature data.) The model of 10 years of current velocity and  
199 temperature over the length of the river is included in the online Supplementary Material.

## 200 *Modeling salmon smolts*

201 *Downstream migration cues.* We simulated movement of smolts entering the  
202 mainstem Connecticut River from eight tributaries located along much of the length of  
203 the river (Fig. 1). We assumed that smolts use temperature to cue initiation of  
204 downstream movement out of their tributaries and into the mainstem of the river (Jonsson  
205 and Ruud-Hansen 1985; Whalen et al. 1999). We simulated a large range of possible  
206 migration trigger temperatures, from 2 to 15 °C, at 0.5 to 1 °C intervals. We used this  
207 large range to allow us to produce a survival reaction norm across a range of trigger

208 temperatures. For any given migration temperature-cue scenario, we assumed all smolts  
209 used the same cue but that there would be some random variability in actual leaving date;  
210 thus, we modeled the number leaving on any date as a Poisson distribution, with the  
211 mean leaving date being the first occurrence of the specific temperature cue.

212 *Mortality rate.* We assumed that temperature influenced mortality rate, either  
213 directly (above lethal temperatures) or indirectly, by influencing physiology, behavior,  
214 and ecology, including presence and consumption by predators. We do not know the  
215 ultimate fate of smolts that are present in the river at very high or low temperatures but  
216 we assume that swimming ability and other physiological responses are impaired at low  
217 temperatures and that high temperatures increase metabolic costs, risk of disease, and  
218 adversely affect other smolt characteristics. To account for temperature effects, our  
219 simulations included a temperature-dependent reduction in daily probability of survival,  
220 in the form of a proportional multiplier  $\tau$ . We assumed a graduated mortality effect as  
221 temperatures dropped below 7 °C or rose above 16 °C, such that  $\tau$  increased linearly from  
222 0 to 1 across temperatures from 2 to 7 °C and decreased linearly from 1 to 0 across  
223 temperatures from 16 to 20 °C. We refer to this set of functions as the “base”  
224 temperature cost functions. We chose to impose the cost of high temperatures at  
225 temperatures above 16 °C because McCormick et al. (1996) showed that salmon may  
226 lose their smolt characteristics and be unable to make the successful transition from fresh  
227 to sea water as temperatures exceed 16 °C. We know much less about the effect of cold  
228 temperatures. We know that development of smolt physiology is severely reduced at low  
229 temperatures (2 °C compared to 10 °C, McCormick et al. 2000), and this would restrict  
230 successful migration, but we do not have estimates of the magnitude of this effect at

231 temperatures between 2 and 10 °C. Fortunately, our simulation results are remarkably  
232 insensitive to the specific function we use to represent the cost of cold temperatures (see  
233 RESULTS and Appendix D).

234         Because we do not have good estimates of mortality as a direct or indirect  
235 function of temperature and because these functions will have obvious importance in  
236 determining simulated smolt success, we repeated simulations using different temperature  
237 cost functions to assess the effect of temperature-dependent mortality estimates on the  
238 qualitative and quantitative patterns in our results. Because of uncertainty in how low  
239 temperatures affect physiology, behavior, and ecology and how these effects may lead  
240 indirectly to effects on mortality, we also ran simulations in which mortality effects were  
241 limited to very low temperatures:  $\tau$  increased linearly from 0 to 1 from 2 to 5 °C (“cold”  
242 scenario). Because there is also uncertainty as to the fate of smolts at high temperatures,  
243 we ran simulations in which  $\tau$  increased linearly from 0 to 1 across temperatures from 18  
244 to 22 °C (“warm” scenario). We chose this as an extreme, allowing smolts to be  
245 successful even at temperatures above which their smolt physiology has been shown to  
246 degrade.. Because we expected that many of our results would be driven by the cost of  
247 being a smolt in the river when the river gets warm, we used this “warm” scenario to  
248 compare our Base model results to a case of extreme tolerance of warm water.

249         Smolts traveling through, over, or around dams experience an increase in risk of  
250 mortality (Stier and Kynard 1986; Amiro et al. 2000; Aarestrup and Koed 2003). Most  
251 obvious is the increase in predation risk below the dam, but other sources of mortality  
252 that may each contribute a small amount to mortality at dams include predation risk in the  
253 pool above the dam (Jepsen et al. 1998), direct effects of passage at the dam, and never

254 actually moving past the dam. While the last of these does not end in immediate  
255 mortality, it prohibits the smolt from progressing all the way to the mouth of the river.  
256 Data on mortality at dams in similar systems are scarce. We assumed a conservatively  
257 low loss of 2.5% (i.e. 2.5% risk of mortality) in passing from the upper reaches of the  
258 dam pool to the river below, as these dams all had downstream passage facilities. This  
259 estimate is similar to that measured by Amiro and Jansen (2000), but much less than the  
260 53% measured by Aarestrup and Koed (2003) and the 30% measured by Croze and  
261 Larinier (1999). To assess the importance of this loss rate to our overall conclusions, we  
262 also ran the model with loss rates at dams of 5%, 10%, and 25%.

263         In addition to all of the sources of mortality described above, we assumed there  
264 was also some background natural mortality. In our base simulations, we assumed a  
265 background daily mortality rate of 0.001. Applied over a year, this would be equivalent  
266 to a 30% mortality rate, within the range of natural annual mortality commonly assumed  
267 in fish populations. Few data exist on natural mortality during downstream migration in  
268 undammed rivers. Recently, Kocik et al (2009) estimated river mortality as 9-32% for  
269 Atlantic salmon smolts in a small river in Maine. While we have no data on background  
270 mortality rates during downstream migration in the Connecticut River or similar rivers,  
271 we considered the possibility that the smolt migration is a naturally high-mortality  
272 process, so we also ran the model with daily mortality rates of 0.005 and 0.01, giving  
273 one-month mortality estimates of 3%, 14% and 26%.

274         *Swimming speed.* In our base model runs, we assumed smolts travel downstream  
275 at the rate of the current, i.e. they move with the velocity of the water (swimming speed,  
276  $\rho = 1$ ). For a 15-cm smolt swimming the entire course of the simulated river on an

277 average day, this is equivalent to moving at about 3.6 body lengths per second. Because  
278 we do not have good estimates of swimming speed in nature, we repeated the simulations  
279 using swimming speeds of one-half ( $\rho = 0.5$ ) and twice ( $\rho = 2$ ) the rate of the current to  
280 assess the effect on the qualitative and quantitative patterns in our results. As a  
281 comparison, Stira reported smolts traveling about 56 km in 24 h (R. Stira, Northeast  
282 Utilities Service Company, personal communication). Without any delay at dams, that  
283 rate would be comparable to our simulated smolts moving at about 0.6 times current  
284 speed, whereas Fangstam (1993) reported average smolt speeds of two times the current  
285 velocity. Thus, our values of  $\rho = 0.5, 1, \text{ and } 2$  span an appropriate range.

286 We assumed smolts moved through the river primarily at night (Thorpe and  
287 Morgan 1978; Moore et al. 1998), so we simulated 12 h of swimming each day. Given  
288 evidence of temperature-dependent daily swimming duration (Ibbotson et al. 2006), we  
289 also simulated smolts swimming 12 h/d until temperatures rose above 12 °C, and then  
290 swimming 24 h/d (Table 1, Model Y).

291 When smolts approach dams, their swimming speeds decline, reflecting the  
292 decrease in current velocity and the confusion of navigating through or around the  
293 structure (Nettles and Gloss 1987; Croze and Larinier 1999; Aarestrup and Koed 2003).  
294 We modeled this as a delay at the dams. We refer to this throughout as "delay" even  
295 though in many altered systems, data are not available on pre-dam conditions. In the  
296 base runs, delay ( $\delta$ ) at an individual dam was set at 0, representing a system without  
297 dams. To assess the effect of delay at dams, we increased  $\delta$  to 0.5, 2, 4, and 8 d. As a  
298 comparison, Aarestrup and Koed (2003) reported delays of 0-9 d at a small weir and  
299 Croze and Larinier (1999) reported delays of 0-12 days. For any given dam-delay

300 scenario, we assumed random variation in actual time until passage, in the form of a  
301 Poisson process, with mean delay =  $\rho$ . While the actual delay at a dam depends on many  
302 factors, one of the most important of which is the characteristics of the dam itself (Castro-  
303 Santos and Haro 2003), we have modeled all dams in a given model run as having the  
304 same Poisson distribution of delays.

305 *Simulation scenarios*

306 Our responses of interest in these simulations were 1) rate of survival of smolts,  
307 where survival was defined as reaching the mouth of the river (i.e., Long Island Sound)  
308 alive and in a condition that would allow successful transition to the sea and 2) optimal  
309 downstream migration-trigger temperature. We designed our “base” model run (model  
310 B, Table 1) to have smolts experiencing no delay at dams ( $\delta = 0$ ), traveling at the speed  
311 of the current ( $\rho = 1$ ), and having daily background mortality rate of 0.001. For this  
312 scenario and all other scenarios, we simulated smolt downstream movement under  
313 different assumptions of migration-trigger temperatures, from 2 to 15 °C. For each  
314 trigger temperature, we simulated smolt movement through ten year-specific templates of  
315 temperature and flow (1993-2002), with five replicate simulations on each annual  
316 template. Within each of these model runs, we simulated 100 smolts leaving a given  
317 tributary, for each of the eight modeled tributaries. We calculated tributary-specific  
318 survival rate from these 100 smolts, for each simulation. To calculate smolt survival over  
319 the entire system of eight tributaries, rather than assuming 100 smolts arise from each  
320 tributary, we weighted the number of smolts from each tributary by the relative number  
321 expected, based on tributary-specific parr population estimates the previous fall (J.  
322 McMenemy, Connecticut River Atlantic Salmon Commission Wild Smolt Estimates,

323 unpublished data). We used a mean of fall estimates from 1996-2002 to arrive at the  
324 relative proportional contribution of each tributary into the pool of downstream migrating  
325 smolts (Appendix B). We present some of the model results for only three tributaries  
326 (Salmon RK 29, West RK 241, and Wells RK 428 rivers; see Fig. 1) that span a broad  
327 range of distance from the mouth of the Connecticut River to allow us to illustrate  
328 specific details of latitudinal trends within the watershed, though all simulations were  
329 carried out for smolts from all tributaries. Data do not exist on numbers of smolts that  
330 successfully exit the river into the estuary, so validating the model with actual smolt  
331 survival data is not possible.

332 *Tributary-specific migration cues and effects of dams.* We generated tributary-  
333 specific survival responses over a range of migration-initiation temperatures for the case  
334 in which no dams were present. We also calculated the whole-system best trigger  
335 temperature, using proportional representation from individual tributaries. We repeated  
336 this set of simulations, incorporating the effects of dams. We included both delay at  
337 dams (0.5, 2, 4, or 8 d delay per dam) and direct mortality at dams (2.5% per dam  
338 encountered). To distinguish the effect of delay from the effect of direct mortality, we  
339 also completed scenarios in which we included delay without the added mortality (Table  
340 1, scenarios FF and II) and direct mortality without delay (Table 1, scenario D).

341 *Effect of swim speed and temperature cost functions.* To test the effects of our  
342 assumptions about swim speed and temperature costs, we completed simulations in which  
343 we varied each of these factors. With delays at dams of 0 (Table 1, scenarios A, B, and  
344 C) and 4 (Table 1, scenarios H, I, and J) days, we simulated smolts swimming at 0.5, 1.0,  
345 and 2.0 times the speed of the current. All other simulations were done with smolts

346 swimming at 1.0 times the speed of the current. With delays at dams of 0, 2, and 4 days,  
347 we simulated smolts experiencing either the “cold” (Table 1, scenarios M, O, and P) or  
348 the “warm” (Table 1, scenarios S, U, and V) temperature cost functions. All other  
349 simulations were done with the “base” temperature costs functions.

350 For all scenarios, results included the optimal trigger temperature (temperature  
351 cue that gave the maximum average survival for the entire system), whole-system  
352 maximum survival (the survival associated with the optimal trigger temperature), whole-  
353 system survival of smolts using a trigger temperature of 7.5 (the optimal trigger  
354 temperature for the Base model, B, with no dams), and tributary-specific survival of  
355 smolts using a trigger temperature of 7.5 °C for three tributaries. We emphasize trigger  
356 temperatures at which survival exceeds 75%.

357 *Effect of mortality rates.* To understand how background daily mortality rate and  
358 rate of direct mortality at dams influenced our conclusions, we ran additional simulations  
359 at higher mortality rates. Changes in background mortality rate obviously will cause  
360 changes in total number of survivors, but we were interested in any qualitative effects  
361 these changes might cause. For example, increasing background daily mortality rate may  
362 enhance the difference in the leaving-time effect on survival between smolts leaving from  
363 upstream tributaries and those leaving from downstream tributaries. Thus, in addition to  
364 our baseline daily mortality of 0.001, we simulated background mortality of 0.005  
365 (Models 9-11, Table 2) and 0.01 (Models 12-14, Table 2) at 0, 2, and 4-d delay at dams,  
366 specifically to see its effect on optimal temperature-cue differences between upstream  
367 and downstream tributaries. Similarly to changes in background mortality rates, changes  
368 in direct mortality at dams obviously will cause changes in total number of survivors in

369 the presence of dams, but we were interested specifically in how these changes would  
370 affect relative numbers of fish dying directly at the dams compared to numbers dying at a  
371 time and location removed from the dam. Thus, in addition to our baseline 2.5%  
372 mortality at dams, we simulated direct dam mortality of 5% (Models 15-18), 10%  
373 (Models 19-22), and 25% (Models 29-32) at 0, 2, 4, and 8 d delay at dams (Table 1).

374

375

## RESULTS

376 Water temperatures in the Connecticut River varied across dates, locations, and  
377 years in a way that potentially affected juvenile salmon survival. Water temperature  
378 increased rapidly during the spring in the Connecticut River (Appendix A). Across years,  
379 water temperature at any given site varied on any date (Appendix A), such that a smolt  
380 using a temperature cue to begin migration might begin at very different times in  
381 different years. While temperature generally increased from upstream to downstream on  
382 any given date (Appendix A), there were many individual dates in individual years in  
383 which breaks from this pattern occurred, with irregular warm or cold spots occurring  
384 within the longitudinal temperature gradient.

385 Smolt survival varied with temperature that cued migration and with tributary of  
386 origin. Smolts from tributaries that entered the mainstem at lower river kilometers (i.e.,  
387 closer to Long Island Sound) had a broad range of temperatures at which they could  
388 begin migration (Fig. 2C). This range was reduced in the uppermost tributaries (Fig. 2A,  
389 2B). If we arbitrarily pick 75% survival as representing good survival, the range of  
390 appropriate migration-cue temperatures increased from 5-10 °C for smolts from the  
391 Wells River (RK 428) to 6-16 °C for smolts from the Salmon River (RK 29). When we

392 consider overall survival for all smolts in the system, weighted by proportional  
393 contributions from each tributary, the range of successful migration-cue temperatures was  
394 still fairly broad, from 5-10.5 °C (Fig. 2D).

395         Even a small delay at dams reduced the range of temperature cues that yielded  
396 high survival for smolts. With a 2-d delay at dams, smolts from upstream tributaries had  
397 no temperature cue that guaranteed high (>75%) survival across all years (Fig. 2E). The  
398 range of temperatures that yielded 75% survival across all years was reduced  
399 substantially at the West River with a small dam delay (Fig. 2F). At the most downstream  
400 tributary, there was no effect of dams because the Salmon River entered the mainstem  
401 river below the first dam (Fig. 2G). With a 2-day delay in dams, over all tributaries, only  
402 a very narrow range of temperature cues (6-8 °C) resulted in at least 75% survival in 9 of  
403 10 years; no temperature cue guaranteed high survival across all years (Fig. 2H).

404         As fish were delayed at dams, survival decreased and the incidence of poor year  
405 classes increased, especially for smolts coming from upriver tributaries. When no delay at  
406 dams (Fig. 3, Model B) was compared to only a 0.5-d delay at dams (Fig. 3, Model K),  
407 mean survival decreased from 97 to 76% for the Wells River (Table 1), and, with this  
408 slight delay at dams, some years had survival near zero. For smolts from the West and  
409 Salmon Rivers, which encountered fewer or no dams, this half-day delay had little or no  
410 effect on survival (Fig. 3, Models B and K). As we increased delays at dams from 0.5 to  
411 8 days (Fig. 3, Models K, F, I, and L), overall survival decreased substantially for Wells  
412 River (from 76% to 0%) and the West River (from 92% to 42%), and not at all for the  
413 Salmon River (as these smolts encounter no dams). For the Wells River and, to a lesser

414 extent, the West River, the number of years with very poor survival increased with the  
415 extent of dam delay.

416         Optimal trigger temperatures varied little across scenarios. For smolts from all  
417 tributaries, in scenarios without dams, either the optimal time to leave was when the  
418 mainstem reached 7.5 °C, or this temperature cue resulted in survival within 10% of the  
419 optimal survival (Table 1). In many cases, a range of temperature cues offered survival  
420 rates very close to that of the optimal temperature, illustrated by the broad plateaus of  
421 high survival in Fig. 2. There was a shift in the absolute optimal migration temperatures  
422 from downstream to upstream tributaries, with optimal leaving times being at lower  
423 temperatures for smolts from upstream tributaries than for smolts from downstream  
424 tributaries. But just as strong was the result that the range of temperatures that yielded  
425 high success narrowed (Fig. 2A-C) from downstream to upstream tributaries. These  
426 patterns were robust to changes in background mortality rate (Appendix C). With a delay  
427 at dams (2 and 4 days, Models F and I), the optimal trigger temperature was the same as  
428 with no delay at dams (7.5 °C; Model B; Table 1). Consequently, the lower survival with  
429 the inclusion of dam delays was the result of both inappropriate migration times and  
430 delays caused by dams.

431         We considered both the direct effect of dams on mortality (modeled as 2.5%  
432 additional mortality with each dam encountered) and the indirect effect of dams on  
433 mortality, which resulted from smolts being delayed at the dams. Both direct and indirect  
434 dam mortality reduced survival of outmigrating smolts. Alone, the 2.5% direct mortality  
435 associated with dams reduced survival for smolts from the Wells River from 97% (Fig 3,  
436 Model B) to 86% (Fig. 3, Model D). Combining this 2.5% direct mortality at dams with

437 a 2-d delay at dams resulted in survival of 65% for smolts from the Wells River (Fig. 3,  
438 Model F). Including only the 2-d delay at dams, but not the 2.5% direct mortality at  
439 dams, resulted in survival of 73% (Model FF, Table 1), suggesting that the indirect effect  
440 of delaying the outward migration of smolts (25% reduction in survival) was at least as  
441 important as the direct effect of mortality at dams (11% reduction in survival). For a 4-d  
442 delay at dams, for smolts from the Wells River, including both the delay and direct effect  
443 of dams resulted in 29% survival (Model I, Table 1). Removing direct mortality increased  
444 survival only to 32% (Model II, Table 1), again suggesting that the indirect effect of dam  
445 delay was a major source of mortality. A similar but smaller effect occurred in the West  
446 River (Model F vs. FF and Model I vs. II, Table 1).

447       Clearly our choice of 2.5% mortality at dams affects the relative numbers of  
448 deaths at dams and away from dams. We see this most strongly in the survival of fish  
449 from the tributaries far upstream. When we considered higher levels of direct mortality  
450 at dams, we found that rate of mortality at dams interacted with delay at dams to  
451 determine the proportion of total deaths occurring at dams for Wells River (RK 428)  
452 smolts (Fig. 4). With increasing rate of direct mortality at each dam, the total number of  
453 deaths at dams increased while the non-dam deaths decreased. With increasing delays at  
454 dams, the non-dam deaths increased relative to the at-dam deaths (Fig. 4). Of the Wells  
455 River smolts surviving direct mortality at dams, non-dam mortality took 10% of these  
456 survivors with a 2-d delay at dams, 37% with a 4-d delay, and 98% with an 8-d delay,  
457 regardless of level of direct dam mortality.

458       To better understand the strong effect of delay at dams on survival, we plotted  
459 temperatures encountered by smolts as they moved through the river. As an illustration

460 of the indirect effect of delay at dams, we show temperatures encountered by 10 smolts  
461 leaving the West River at 10 °C in 2001, with and without dams (Fig. 5). Indirect  
462 mortality was related not just to time in the river but also to increased chances of  
463 encountering “warm patches” downstream (Fig. 5). Given the temperature mosaic that  
464 occurs between the West River and Long Island Sound in the spring, smolts that left the  
465 West River at 10 °C and encountered no dam delays exited the river quickly and  
466 experienced moderate temperatures (Fig. 5A). When the same fish were delayed by  
467 dams, mortality occurred (Fig. 5B). Some fish died at the dams, but many more died  
468 after they successfully negotiated the dams, as they encountered warm patches of water  
469 downstream. Consequently, it is the combination of the delay and increasing water  
470 temperatures through the season that is responsible for the indirect mortality associated  
471 with dam delay.

472         To assess how sensitive our simulation results were to our choice of swim speed,  
473 we re-ran the simulation with different swim speeds. Altering swim speed had a limited  
474 effect on survival, except for smolts coming from the most upstream tributaries.  
475 Reducing swim speed by half had little effect on survival in most years in most tributaries  
476 (Fig. 6, Model B vs. Model A), although it increased the likelihood of having years of  
477 very poor survival in smolts from the most upstream tributary (Wells River, Fig. 6,  
478 Model A). With no dams, doubling swim speed affected survival little, probably because  
479 survival was high already (Fig. 6, Model B vs. Model C). The reduction in survival  
480 associated with a 4-d delay at dams was exacerbated by a slower swim speed (Fig. 6,  
481 Model I vs. Model H), with year-class failures occurring in most years in smolts from the  
482 Wells River (Fig. 6, Model H). A doubling of swim speed, with 4-d delays at dams,

483 increased survival of smolts from the Wells River, but only to a mean survival of 52%  
484 (Fig. 6, Model J). When we included an environmentally cued increase in swim time  
485 (Fig. 6, Model Y), we saw survival patterns similar to those with a doubling of swim  
486 speed (Fig. 6, Model J). Overall, the choice of swim speed used in the simulations  
487 affected mean survival of smolts only from upper tributaries, but it did not change the  
488 pattern of the effect of dams on survival in these smolts.

489 To assess how sensitive our results were to the parameters in our temperature-cost  
490 functions, we re-ran the simulations using different cost functions. In Models M, O, and  
491 P, we made very cold temperatures (2-5 °C) more costly and somewhat cold temperatures  
492 (5-7 °C) less costly than in our original models B, F, and I. Changing the cold-cost  
493 function changed survival very little, regardless of delay at dams (Table 1; Appendix D).  
494 In Models S, U, and V, we made smolts less sensitive to warm temperatures, specifically  
495 including no costs of moderately warm temperatures (16-18°C), at which smolts incurred  
496 survival costs in other simulations. When there were no dams, the warm-cost function  
497 did not alter results (Table 1; Appendix D). When the warm-cost function was combined  
498 with delays at dams, survival still decreased as a result of the delay, but not as much as in  
499 models using the original temperature cost functions (Appendix D).

500

501

## DISCUSSION

502 Dams can cause mortality of downstream migrating fish at or near the dam at the  
503 time of passage as well as under circumstances spatially and temporally removed from  
504 the dam. In our model, when a multi-day delay occurred at multiple dams, the number of  
505 Atlantic salmon smolts dying downstream of the dams was comparable to the number

506 dying at the dams themselves because of the likelihood of encountering warm  
507 temperatures in the lower river following dam delay. Fish can be delayed at dams  
508 because reduced velocity above dams creates reservoirs  
509 (Søndergaard and Jeppesen 2007) that slow downstream migration (Clarke et al. 2007)  
510 and alter flow paths, concealing appropriate migratory routes past dams. Much research  
511 has focused on how to design dam passageways that attract downstream migrants (e.g.,  
512 Pacific lampreys *Lampetra tridentata*, Moser et al. 2002; eels *Anguilla anguilla*, Gossett  
513 et al. 2005; Atlantic salmon and American shad *Alosa sapidissima*, Haro et al. 1998), as  
514 hydropower regulations typically focus on mortality at the immediate dam site (e.g.,  
515 spillway, turbines, bypass). The results from our larger-scale downstream-movement  
516 model suggest that delay at dams can cause mortality at a time and place removed from  
517 the dam, a result also suggested by the analysis of Chinook salmon in the Columbia River  
518 by Kareiva et al. (2000). Dam impacts must be considered at a broader spatial and  
519 temporal scale than is currently the standard practice.

520 Dams that delay migration can reduce migrant success by (1) requiring additional  
521 energy expenditure, making the migration energetically impossible to complete or  
522 resulting in the migrant arriving to its destination with low energy reserves, or (2) causing  
523 a mismatch between the evolutionarily selected timing of migration and environmental  
524 conditions en route or at the migration endpoint. Caudill et al. (2007) suggested that the  
525 first of these mechanisms may have been at least partially responsible for their observed  
526 field pattern of a negative correlation between duration of time spent at dams and  
527 ultimate success of the migrant (upstream migrating adult Pacific salmon *Oncorhynchus*  
528 spp.). Similarly, Acou et al. (2008) propose that the ultimate cost of delays at dams

529 experienced by downstream-migrating eels is poor energetic condition by the time they  
530 reach the sea. Budy et al. (2002) demonstrate that downstream migrating salmonids in  
531 the Snake River suffer delayed mortality as a result of accumulated stress from  
532 navigating multiple hydroelectric dams on their journey to the ocean. Our model results  
533 provide one of the few examples of the second mechanism by which delays at dams  
534 reduce migration success, that is, by introducing mismatches between timing and  
535 environmental conditions. Similar mismatches have been suggested to be a significant  
536 contributor to the decline of Pacific salmon (e.g., Waples et al. 2007). Understanding and  
537 quantifying the potential costs associated with taking extra time to successfully navigate a  
538 migration-route barrier requires further attention for both anadromous fish and other taxa  
539 encountering barriers to migration.

540 Indirect effects of delays at barriers may affect a range of migratory taxa in both  
541 aquatic and terrestrial systems. Much recent work has focused on the direct effects that  
542 occur when anthropogenic barriers stop individuals from completing migrations, either as  
543 a result of behavioral avoidance of barriers (e.g., road avoidance by terrestrial reptiles,  
544 Shepard et al. 2008; road/pipeline avoidance by caribou *Rangifer tarandus granti*,  
545 Cameron et al. 2005) or as a result of mortality (e.g., road mortality of turtles, Aresco  
546 2005). These direct effects are obvious and often very strong. For example, Aresco  
547 (2005) predicted that 98% of turtles crossing a Florida highway would have been killed in  
548 the absence of human intervention. The east-west migration of Mongolian gazelle  
549 (*Procapra gutturosa*) may have been completely shut down by the construction of a  
550 railroad (Ito et al. 2005). In those systems, researchers have not yet addressed the  
551 potential indirect effect of barriers on the ultimate success of migrants that make it past

552 them. Insights from our simulations suggest that current efforts to construct passageways  
553 over, under, or around barriers, such as underpasses on Arctic oil pipeline to allow  
554 passage of migrating caribou, may benefit from considering these potential indirect  
555 effects of successful, but delayed passage. For example, when seaward migration of land  
556 crabs is interrupted by roads, they take a longer migration route and experience  
557 energetically expensive exposure to high temperatures and desiccation (Adamczewska  
558 and Morris 2001). So while many of the crabs survive the road crossing, their ultimate  
559 endurance may be reduced (Adamczewska and Morris 2001). To develop analyses  
560 similar to ours to understand the relative importance of direct and indirect effects of  
561 barriers in other taxa would require an understanding of (1) what selection pressures  
562 drive timing of migration as well as the consequences of altering that timing and/or (2)  
563 the consequences of reduced energetic condition upon completion of migration that may  
564 result from delay

565         High temperatures are particularly important to coldwater (McCullough et al.  
566 2009) and diadromous species (Lassalle et al. 2008), especially Atlantic salmon smolts  
567 that must exit freshwater before downstream river temperatures become too warm. In the  
568 Connecticut River, a system which has a long north to south trajectory in which water  
569 temperatures increase from upstream to downstream, Atlantic salmon are at the southern  
570 edge of their range in North America (Parrish et al. 1998) and timing of smolt migration  
571 is critical. Our study suggests that temperature “hot spots” in the Connecticut River,  
572 possibly caused by water entering from warmer tributaries in sub-basins with agricultural  
573 and urban riparian areas, may play an important role in the influence of dams on smolt  
574 migration success. Unpredictable heterogeneities in temperature are likely to develop

575 when tributaries drain areas with different land uses that are subjected to variable degrees  
576 of solar heating. It is also possible that smolts use cool spots in the river as refuges from  
577 warm temperatures, though it is not clear how long smolts would be able to stall their  
578 migration in these refuges. In addition to the hot spots included in our simulations, the  
579 Connecticut River has hot spots arising from river water being used as cooling water for  
580 power plants; we chose not to include these hotspots in our simulations. The fact that  
581 temperature hotspots arose in our simulated river, even with a coarse spatial  
582 representation of temperature and omission of extreme effects on temperature from  
583 power plants, points to the simulation as being a conservative reflection of the actual  
584 potential for hotspots. Smolts that encounter these warm temperature patches may lose  
585 their smolt characteristics (McCormick et al. 1996), cease downstream movement  
586 (Zydlewski et al. 2005), and are presumed to die shortly thereafter. With climate change  
587 models predicting higher Connecticut River water temperatures in the future, this  
588 problem will only intensify in severity.

589         When we began this study, we expected to see optimal timing of migration to be  
590 earlier (i.e., cued by lower temperatures) for smolts from upstream tributaries than those  
591 beginning their journeys much closer to the mouth of the river. This pattern was seen in  
592 Atlantic salmon in Scotland and was shown to have a genetic basis (Stewart et al. 2006).  
593 Other studies have shown genetically based population-specific migration timing in  
594 Atlantic salmon smolts, though these data have not been analyzed in relation to distance  
595 of the population from the mouth of the river (Orciari and Leonard 1996; Nielsen et al.  
596 2001). In addition to seeing this shift in optimal migration timing from upstream to  
597 downstream, we also saw a shift in the breadth of temperature cues that resulted in high

598 survival. Only a narrow range of migration temperatures gave good survival for smolts  
599 from upper tributaries; these same temperatures also gave excellent survival for smolts  
600 from lower tributaries, but smolts from lower tributaries had a broad range of  
601 temperatures at which they could begin a successful migration. This suggests the  
602 potential for stronger selection for specific migration timing in some populations (those  
603 with farther to travel) than in others, rather than for equally strong selection for different  
604 timing among populations. The narrowness of the range of appropriate migration-  
605 initiation temperatures for smolts from upstream tributaries is a function of the year-to-  
606 year variation in flow and temperature conditions. In any given year, there may be a  
607 broad range of migration times that would result in high survival, even for smolts from  
608 upstream tributaries. However, across years, this temperature range shifts, resulting in  
609 only a narrow range of migration times that are appropriate in all years. Thus, these  
610 upstream populations are extremely vulnerable to longterm changes in patterns of  
611 temperature and flow in the river. The template of historical and current environmental  
612 variation is essential context for the interpretation of within- and across-system migration  
613 timing and cues.

614         Successful long distance migration requires that evolutionary adaptations be  
615 matched with environmental conditions. For salmon smolts, physiological and  
616 behavioral “smolt windows” must mesh so that organisms are ready to survive saltwater  
617 at the same time they reach the estuary, using cues that allow them to successfully transit  
618 existing environmental pathways. Where restoration programs have used hatcheries or  
619 translocation across systems, physiological and behavioral “smolt windows” may have  
620 become decoupled, and cues for movement no longer match the environmental conditions

621 that provide the best survival (Hendry et al. 2003). Where possible, restoration programs  
622 should allow for local adaptations in migration timing, though this is often not feasible.  
623 Even for locally adapted populations, optimal migration timing may shift if there has  
624 been a consistent shift in temperatures from historical means (e.g., Atlantic salmon,  
625 Kennedy and Crozier 2010; pied flycatcher *Ficedula hypoleuca* Both et al. 2006).  
626 Barriers to migration and consequent delays will further complicate the difficulty of  
627 matching evolutionary adaptations, as will environmental changes associated with  
628 climate change. For example, we would not necessarily expect populations that were  
629 locally adapted for successful migration from specific tributaries to maintain that local  
630 advantage in the face of changing temperature and flow regimes. Interactions among  
631 migration barriers, disruption of local adaptation, and changing cues and conditions have  
632 widespread implications for conservation.

633         Our results showing adverse consequences for migrating animals, even after they  
634 successfully pass a barrier, suggest different ways of thinking about restoration of salmon  
635 and other anadromous fish into coastal watersheds. Fullerton et al. (2009) suggest that  
636 managers consider a suite of potential targets of their actions in addressing the negative  
637 impact of migration barriers. First, and most obvious, removal of the barriers themselves  
638 would eliminate the adverse consequences for migrating animals, but this is often either  
639 impossible or impractical, so we must consider alternatives. Because delays at dams  
640 cause salmon smolts to encounter too-warm temperatures upon their arrival at the estuary  
641 later in the season, selecting for stocks having earlier downstream movements has been  
642 suggested as a possible solution. Our simulation results show, however, that the effects  
643 of dams is not due only to inappropriate migration-initiation cues, but also to year-to-year

644 unpredictability in timing and location of patches of warm water, with extended river  
645 residence times increasing the chances of encountering one of these patches. A third  
646 solution is to reduce the delay associated with the barriers. For downstream migrating  
647 salmon, survival and immediate transit time through different fishway, bypass, and  
648 spillway configurations has been intensively examined. However, time that animals take  
649 to transit the larger dam impact area, from the first slowing of current velocity upriver of  
650 the dam to resumption of river habitat below the dam, has not been a focus of fish  
651 passage and river restoration efforts for Atlantic salmon (though this has begun to be  
652 studied in Pacific salmon, e.g., Welch et al. 2008). Our results suggest that a larger  
653 spatial and temporal definition of dam impact is needed. Delays in this larger impact  
654 zone must be quantified and reduced where possible. Finally, environmental managers  
655 can address environmental conditions encountered after and as a result of the delays at  
656 barriers. For downstream migrating fish, occurrences of temperature hotspots may be  
657 affected by landuse and runoff, a potential link that requires further study.

658         Our simulations provided us with strong qualitative insight into the potential  
659 effects of dams on smolt migration success, including the strength of the effect of delay at  
660 dams on survival, the effect of annual variation in river conditions on optimal migration  
661 temperatures, and the pattern of survival and optimal temperature cues expected among  
662 populations originating in different tributaries, but it did not give us precise quantitative  
663 estimates of these responses for the Connecticut River. Our simulations were a  
664 simplification of the spatial heterogeneities along the course of the river, presenting only  
665 a coarse spatial picture of flow and temperature and treating the effect of all dams as  
666 equivalent. In fact, salmon movements are surely affected by smaller-scale patterns in

667 flow, and we expect that dams differ in their effect on mortality and delay of smolts  
668 (Laine et al. 2002), based on the specific structure of the dam and the rate of discharge.  
669 Changing to a finer spatial scale would only increase the patchiness of the thermal  
670 environment, and using more dam-specific parameters would not change the general  
671 result that dams cause delays and delays have effects on likelihood of completing  
672 migration. Our estimates of direct mortality at dams and extent of delay at dams were  
673 conservative in comparison to many of the published values, reflecting what the local  
674 biologists and managers felt were more appropriate for this system. Despite using these  
675 conservative estimates, we saw strong negative effects of dams on smolt success.

#### 676 SUMMARY

677 Disruption of migrations due to barriers is being recognized across taxa and  
678 ecosystems. Population conservation and restoration has been focused on removing  
679 barriers or facilitating animal movement around or through these barriers. Our study  
680 suggests that this local view of the effect of barriers, while important, may be  
681 insufficient. Even in the face of successful passage around barriers, migrants may be  
682 delayed sufficiently to cause a mismatch in their physiological and energetic state and the  
683 environmental conditions en route and at the migration destination. To successfully  
684 manage these migrating populations, our results suggest that we should consider effects  
685 over a broad geographic and temporal footprint of the barrier, and not limit ourselves to  
686 management only of the barrier itself.

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900

901 Table 1. Model scenarios and survival results. Scenarios are defined by downstream  
902 swimming speed of smolts (multiplier of ambient current speed), swimming delay at  
903 dams (d), temperature-dependent survival multiplier (both warm and cold temperatures),  
904 amount of time spent swimming each day, and mortality probability at each dam (%).  
905 Survival results include the trigger temperature that produced the maximum whole-  
906 system survival (“optimal trigger temperature”), the whole-system survival associated  
907 with this trigger temperature (“maximum survival”), whole system survival with a trigger  
908 temperature of 7.5° C (optimal trigger temperature with no dams in the base model run,  
909 scenario B), and tributary-specific survival with a trigger temperature of 7.5°C for the  
910 Wells (RK 428), West (RK 241), and Salmon (RK 29) rivers.

Model scenarios							Survival Results					
Model	Swim Speed	Dam Delay (d)	COLD Cost Function	WARM Cost Function	Swim Time	Mortality at Dam (%)	optimal trigger temp	maximum survival	Survival at 7.5° trigger			
									whole system	Wells R.	West R.	Salmon R.
A	0.5	0	base <sup>6</sup>	base <sup>7</sup>	12 h/d	0.0	6.5	96	95	69	97	98
B	1	0	base	base	12 h/d	0.0	7.5	99	99	97	99	98
C	2	0	base	base	12 h/d	0.0	9.5	99.5	99	99	99.7	97
D	1	0	base	base	12 h/d	2.5	8.5	96	96	86	92	97
F	1	2	base	base	12 h/d	2.5	7.5	88	88	65	83	98
FF	1	2	base	base	12 h/d	0	7.0	92	92	73	90	98
H	0.5	4	base	base	12 h/d	2.5	6.5	72	70	6	63	97
I	1	4	base	base	12 h/d	2.5	7.5	80	80	29	75	98
II	1	4	base	base	12 h/d	0	7.5	84	84	32	80	98
J	2	4	base	base	12 h/d	2.5	7.5	84	84	52	77	98
K	1	0.5	base	base	12 h/d	2.5	7.0	93	93	76	92	98
L	1	8	base	base	12 h/d	2.5	6.5	60	60	0	42	98
M	1	0	cold <sup>8</sup>	base	12 h/d	0.0	6.0	99	99	98	99	99.9
O	1	2	cold	base	12 h/d	2.5	5.5	93	88	65	83	99.8
P	1	4	cold	base	12 h/d	2.5	6.0	87	81	29	74	99.8
S	1	0	base	warm <sup>9</sup>	12 h/d	0.0	9.0	99	99	99	99	98
U	1	2	base	warm	12 h/d	2.5	8.0	94	93	85	90	98
V	1	4	base	warm	12 h/d	2.5	7.5	92	92	68	89	98
Y	1	4	base	base	temp-dep <sup>10</sup>	2.5	7.5	85	85	98	79	48

<sup>6</sup> Base: temperature-dependent multiplier on daily probability of survival increased linearly from 0 to 1 across temperatures from 2° to 7°

<sup>7</sup> Base: temperature-dependent multiplier on daily probability of survival decreased linearly from 1 to 0 across temperatures from 16° to 20°

<sup>8</sup> Cold: temperature-dependent multiplier on daily probability of survival increased linearly from 0 to 1 across temperatures from 2° to 4°

<sup>9</sup> Warm: temperature-dependent multiplier on daily probability of survival decreased linearly from 1 to 0 across temperatures from 18° to 22°

<sup>10</sup> Temperature dependent: smolts swam 12h/d until the temperature rose above 12° C, then swam 24 h/d

911 Table 2. Mortality sensitivity model scenarios. Scenarios are defined by background  
 912 daily mortality, swimming delay at each dam (d), and mortality probability at each dam  
 913 (%). All other parameters are as in the Base model (B). Several of the mortality  
 914 sensitivity models are identical to previously described models; these are denoted  
 915 parenthetically with the model designation from Table 1.

916

**Mortality Model Scenarios**

<b>Model</b>	<b>Background Mortality</b>	<b>Dam Delay (d)</b>	<b>Mortality at Dam (%)</b>
<b>1 (B)</b>	0.001	0	0
<b>2 (FF)</b>	0.001	2	0
<b>3 (II)</b>	0.001	4	0
<b>4</b>	0.001	8	0
<b>5 (D)</b>	0.001	0	2.5
<b>6 (F)</b>	0.001	2	2.5
<b>7 (I)</b>	0.001	4	2.5
<b>8 (L)</b>	0.001	8	2.5
<b>9</b>	0.005	0	2.5
<b>10</b>	0.005	2	2.5
<b>11</b>	0.005	4	2.5
<b>12</b>	0.01	0	2.5
<b>13</b>	0.01	2	2.5
<b>14</b>	0.01	4	2.5
<b>15</b>	0.001	0	5.0
<b>16</b>	0.001	2	5.0
<b>17</b>	0.001	4	5.0
<b>18</b>	0.001	8	5.0
<b>19</b>	0.001	0	10.0
<b>20</b>	0.001	2	10.0
<b>21</b>	0.001	4	10.0
<b>22</b>	0.001	8	10.0
<b>29</b>	0.001	0	25.0
<b>30</b>	0.001	2	25.0
<b>31</b>	0.001	4	25.0
<b>32</b>	0.001	8	25.0

917

918 Fig. 1. Location of the Connecticut River drainage within the four basin states,  
919 Connecticut, Massachusetts, Vermont, and New Hampshire. The eight drainages (and  
920 the distance upstream from the mouth of the Connecticut River, km, for each) from which  
921 our simulated salmon initiated downstream migration to the ocean are indicated with  
922 labels on the left. Dams (and their distance from the mouth, km) potentially affecting  
923 smolt movement through our study reach are indicated with labels on the right.

924

925 Fig. 2. Percent survival associated with smolts leaving their tributaries at specific  
926 temperature cues, for simulations without dams (left panels) and with 2-d delay at dams  
927 (right panels). Results are shown for smolts migrating from the Wells River (RK 428;  
928 panels A, E), West River (RK 241; panels B, F), Salmon River (RK 29; panels C, G), and  
929 the mean for all tributaries combined (panels D, H). Solid lines represent results for  
930 separate years of flow and temperature conditions; dashed lines represent means of all  
931 years. Horizontal bars on the  $x$ -axis show trigger temperatures that resulted in at least  
932 75% survival of downstream migrating smolts.

933

934 Fig. 3. Survival frequency histograms for simulated smolts from three tributaries (Wells,  
935 West, and Salmon rivers) to illustrate the effects of dams on smolt downstream migration  
936 survival. Survival frequencies for each panel include results from five replicate runs for  
937 each of 10 year-specific flow and temperature conditions. Panels are referred to by the  
938 models they represent (Table 1). Percents in the figure legends refer to mean survival  
939 over all replicates and years. Model B is the base model, with no dams. Models K (0.5-d  
940 delay), F (2-d delay), I (4-d delay), and L (8-d delay) include both delay at dams and a

941 2.5% mortality at each dam encountered. Model D includes only the 2.5% mortality and  
942 no delay at dams.

943

944 Fig. 4. Number of deaths (of 500 initial simulated migrants) directly at dams and at times  
945 and locations removed from dams for smolts from the Wells River (RK 428) at five  
946 levels of direct mortality at dams. From top to bottom, panels represent simulations with  
947 2-d, 4-d, and 8-d delays at each dam. Note that Wells River smolts must pass five dams  
948 on their migration down the Connecticut River.

949

950 Fig. 5. Spatial-temporal “map” of temperatures encountered by 10 simulated smolts  
951 leaving the West River at 10 °C to migrate downstream, in temperature and flow  
952 conditions representing 2001. Light horizontal lines indicate locations of dams. Red  
953 lines represent the location of smolts on each day. Note that some paths of some smolts  
954 overlap such that all paths are not visible. Red circles with an X indicate the date and  
955 location of a simulated smolt mortality. A) no dams; in this example, all 10 smolts  
956 survived the migration. B) 2-d delay and 2.5% mortality at dams; in this example, at  
957 least 1 smolt died at a dam, at least 3 smolts died in warm spots downstream of the dams,  
958 and at least 3 smolts survived the migration.

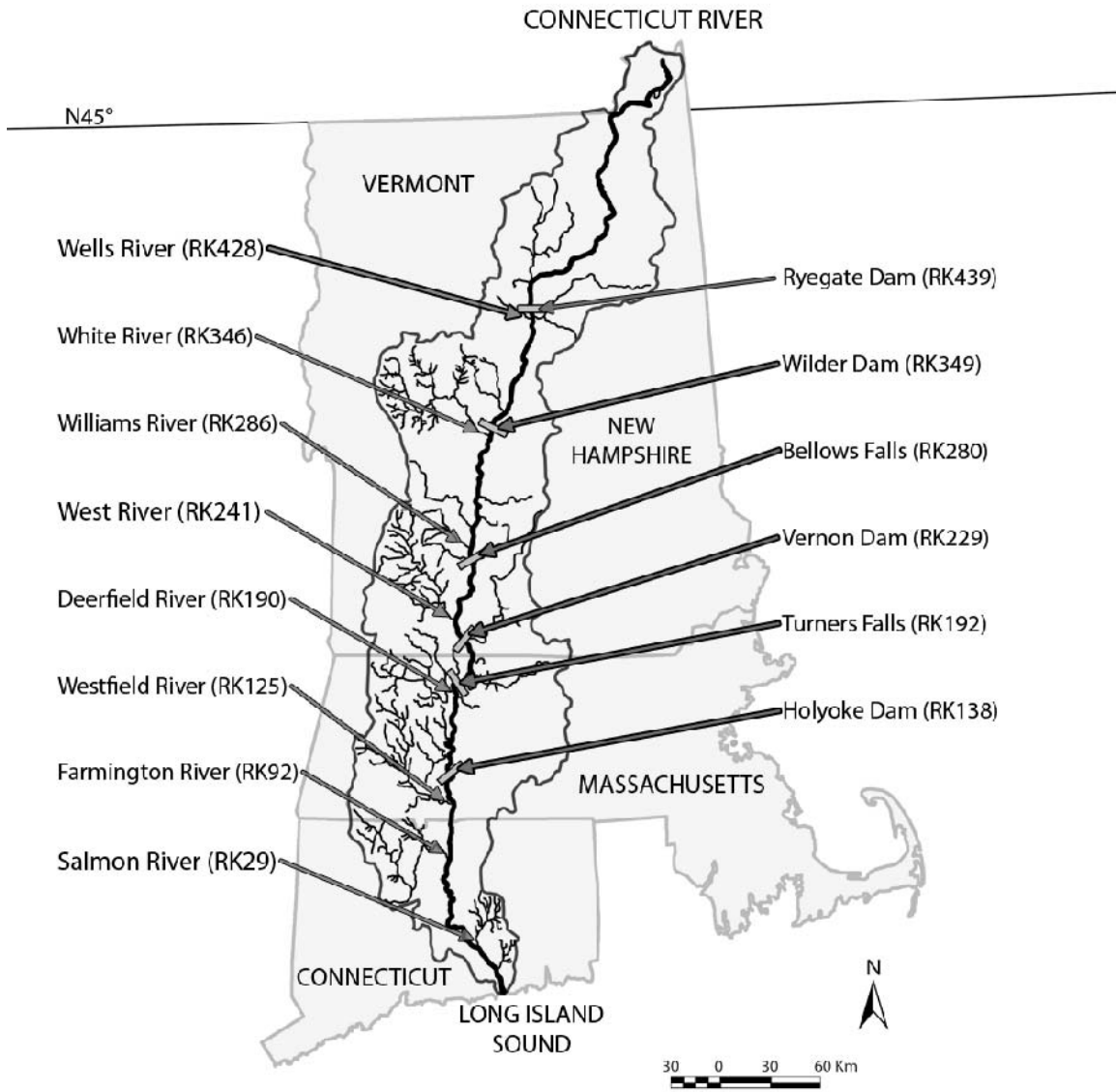
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960 Fig. 6. Survival frequency histograms for simulated smolts from three tributaries (Wells,  
961 West, and Salmon rivers) to illustrate the effects of swim speed on smolt downstream  
962 migration survival without dams (left panels) and with 4-d delay at dams (right panels).  
963 Survival frequencies for each panel include results from five replicate runs for each of 10

964 year-specific flow and temperature conditions. Panels are referred to by the models they  
965 represent (Table 1). Percents in the figure legends refer to mean survival over all  
966 replicates and years. Models A, B, and C have no dams, with swim speeds of 0.5, 1, and  
967 2 times the current. Model H, I, and J have a 4-d delay at dams, with swim speeds of  
968 0.5, 1, and 2 times the current. Model Y has a temperature dependent swim time in which  
969 smolts swim 12 h/d until the temperature rises above 12 °C, after which smolts swim 24  
970 h/d.

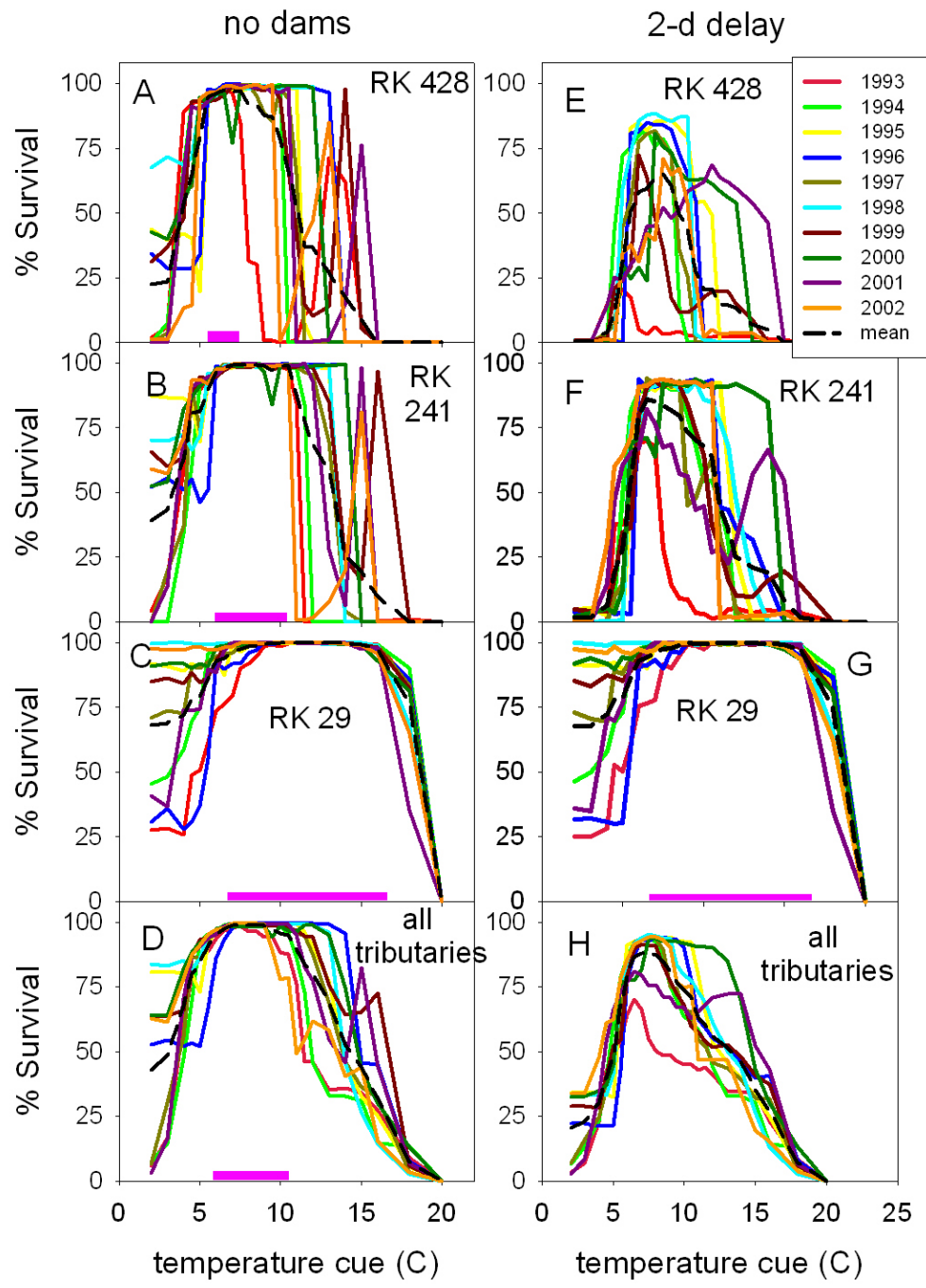
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973  
974 Fig. 1

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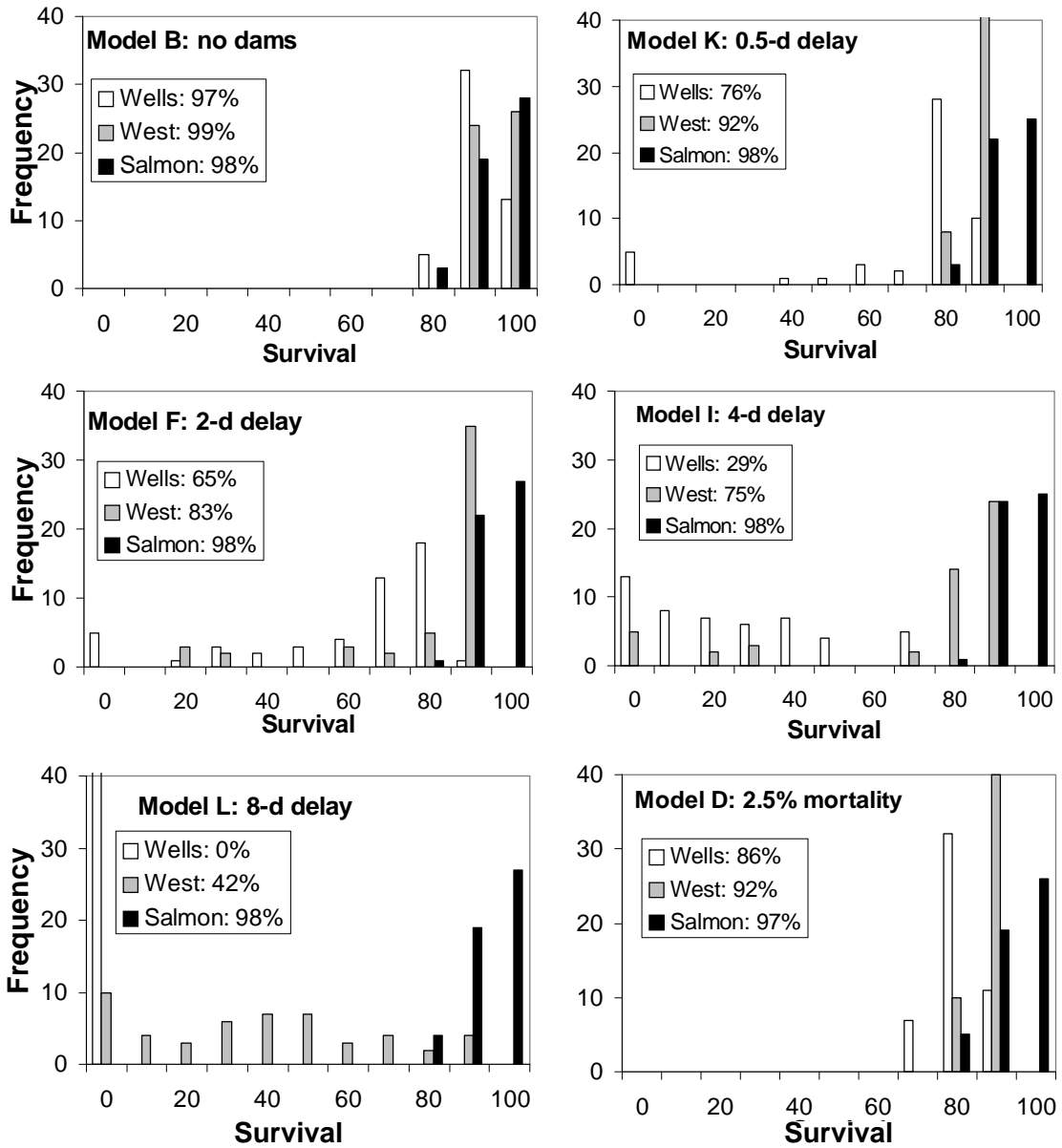


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977 Fig. 2.

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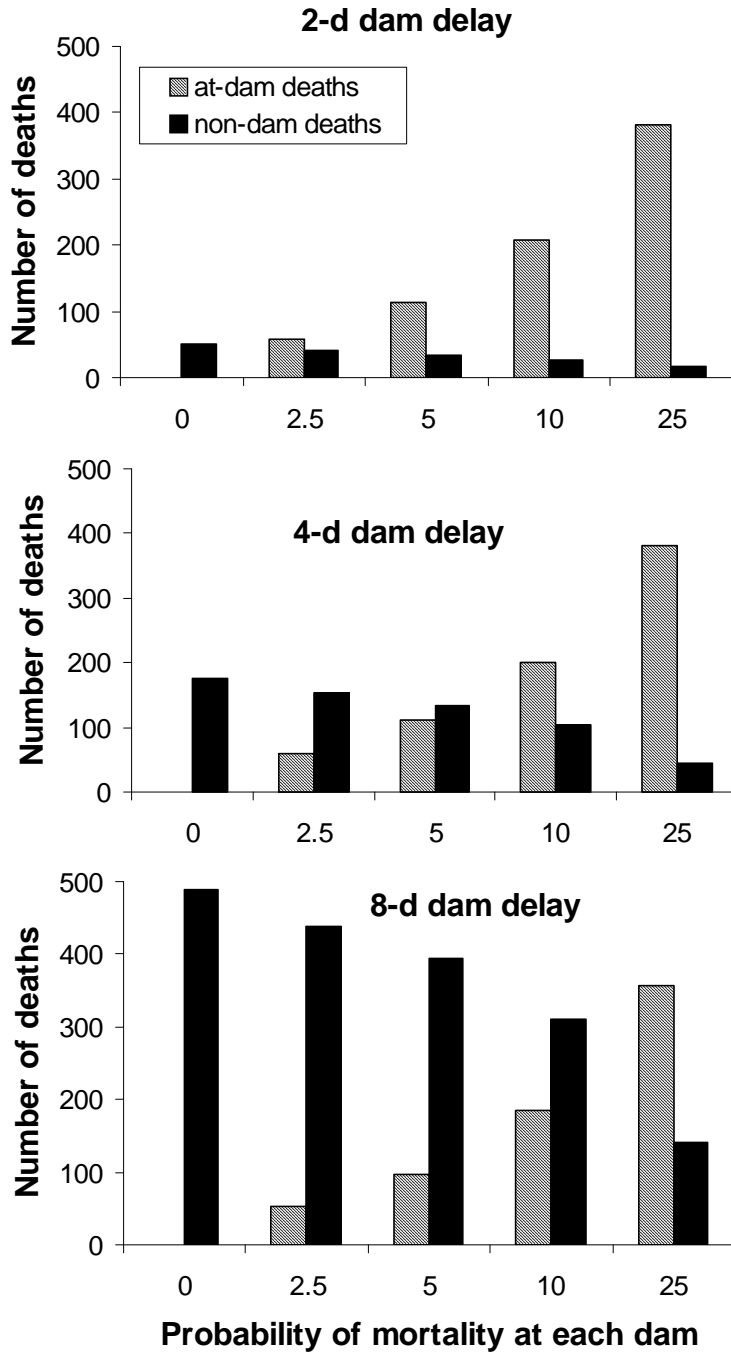


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982 Fig. 3.

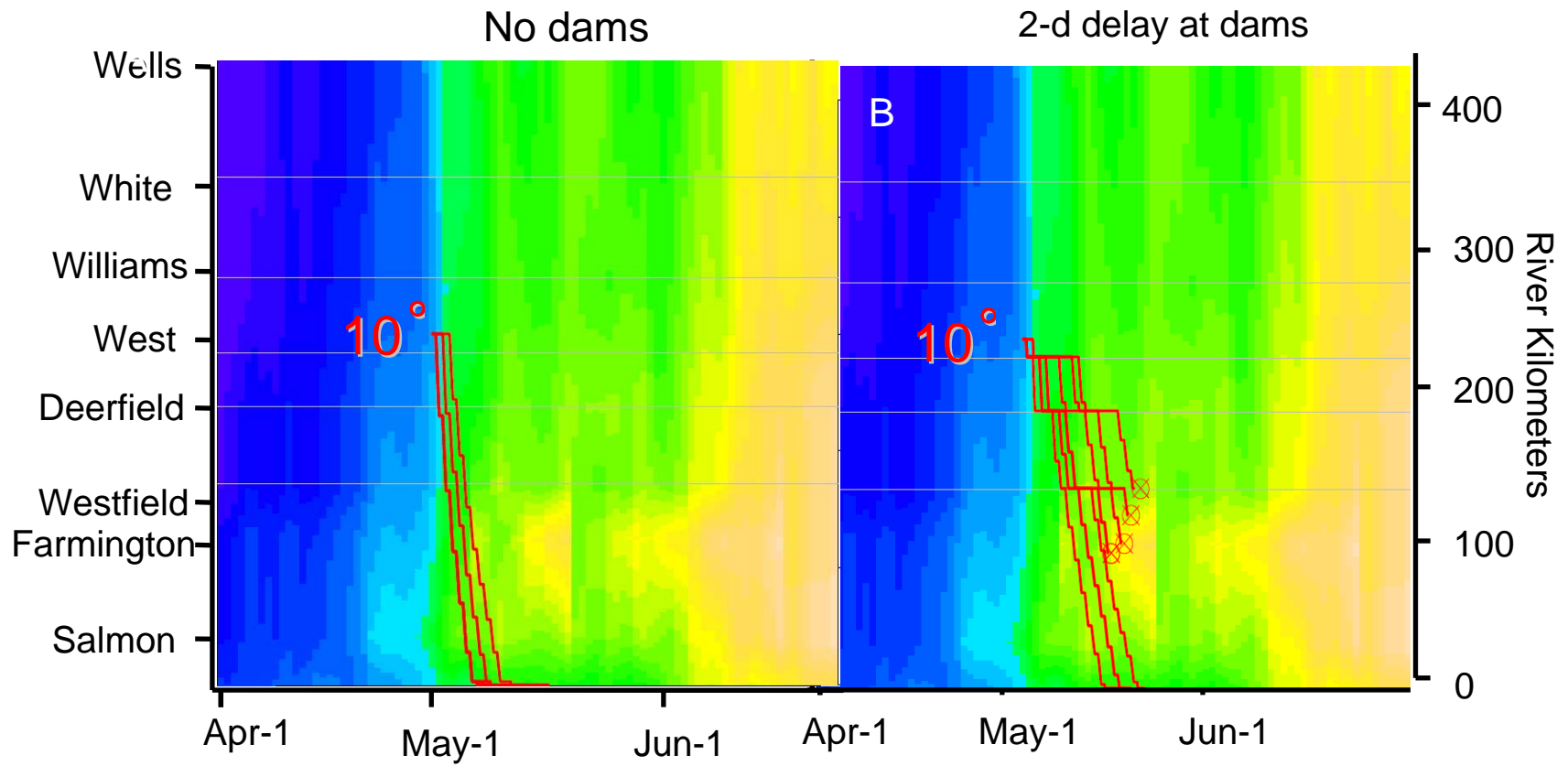
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985 Figure 4

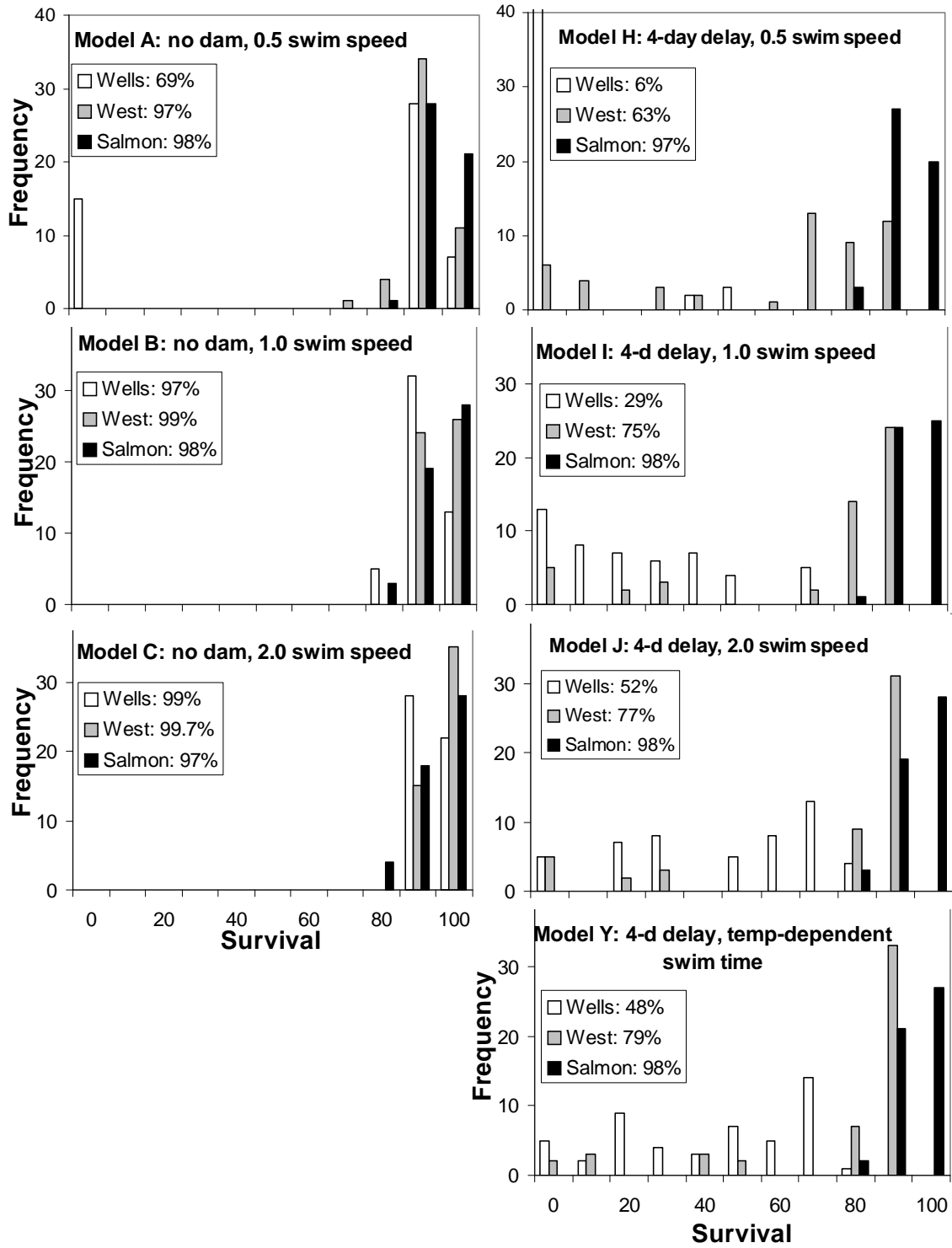
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989 Fig. 5



990

991 Fig. 6

992

1 **Appendix A**

2 We modeled the river as consisting of 1.6-km segments, with temperature and flow  
3 updated daily.

4 *Modeling flow*

5 Our goal was to represent the large-scale spatial patterns in flow over the course of a long  
6 river and the intraseasonal and interannual variation in these large-scale patterns. As  
7 such, we were not interested in representing flow on a fine spatial scale, but focused on  
8 representing how it changed over the migration season and how this varied across years.

9 Flow data, in the form of river discharge values, were obtained from the United States

10 Geological Services (USGS) National Water Information System

11 (<http://waterdata.usgs.gov/nwis>). Although some discharge data exist for many sites, we

12 were limited to using those sites that had sufficient data over the spring migration period

13 (April-June) for each of the years 1993-2002. This span of years was chosen because it

14 was the ten-year period with the most complete data available. We ultimately used data

15 from four sites: Ryegate, VT (near mouth of Wells River, RK 428); West Lebanon, NH

16 (below White River, RK 346); Montague City, MA (Turners Falls, RK 191); and

17 Thompsonville, CT (RK 101). Because current velocity (linear distance per time) is

18 more relevant to smolt movement than is discharge (volume per time), we converted

19 discharge data to current velocity by dividing by the cross-sectional area of the river near

20 each discharge monitoring site. The USGS data include measurements that allow

21 calculation of cross-sectional stream area at different discharge levels, allowing

22 estimation of a function converting discharge to velocity at each site (Table A1). We

23 used linear interpolation over RK to coarsely represent spatial patterns in current velocity

24 along the course of the river, ignoring dams, between monitoring sites. We used velocity  
25 from our most downstream site (RK 101) to represent velocity between this site and RK  
26 0. Upon this flow template, we added dams. We included Wilder Dam (RK 349),  
27 Bellows Falls (RK 280), Vernon Dam (RK 229), Turners Falls (RK 192), and Holyoke  
28 Dam (RK 138). In practice, rather than modeling a dam's effect on current velocity, we  
29 modeled its effect on smolt movement rates relative to the background flow of the river.  
30 In all simulations, we included a short delay, modeled as a Poisson distribution with a  
31 mean of 0.5 d, at the mouth of the river, as the smolts entered the estuary.

### 32 *Modeling temperature*

33 Our goal was to represent the large-scale spatial patterns in temperature over the course  
34 of a long river and the intraseasonal and interannual variation in these large-scale  
35 patterns. As with flow, we were not interested in fine-scale spatial patterns in  
36 temperature. We focused on characterizing the general trends from upstream to  
37 downstream in temperature as well as how temperature changed over the migration  
38 season and varied across years. We used mean daily temperature data from seven sites  
39 along the course of the river. Data sets for some sites were missing certain days, weeks,  
40 and, in some cases, years. If the gaps in data were short (less than seven days), we  
41 interpolated between values from surrounding days. For longer data gaps, which tended  
42 to occur very early and very late in the season, we took advantage of the fact that daily  
43 temperatures at a given site were correlated with temperatures at the next closest site  
44 during individual seasons. For each two-week period, we calculated the mean  
45 temperature difference between two sites and used this to fill temporal gaps in the  
46 temperature data. We used data from the USGS National Water Information System for

47 sites at Connecticut River below Indian Stream, near Pittsburg, NH (RK 605.9) and  
48 Connecticut River at North Stratford, NH (RK 554) and at Thompsonville (RK 101).  
49 Temperatures for Holyoke (RK 138) and Turners Falls (RK 192) were given to us by the  
50 Massachusetts Division of Fisheries and Wildlife. Temperatures for Long Island Sound,  
51 the mouth of the Connecticut River (RK 0), came from a NOAA buoy. Connecticut  
52 Yankee, located at RK 21, provided us with those temperatures, and the Vermont Agency  
53 of Natural Resources gave us temperature data for RK 272 (above Vermont Yankee).  
54 The model of 10 years of current velocity and temperature over the length of the river is  
55 included in the online Supplementary Material.

56 Water temperatures in the Connecticut River varied across dates, locations, and  
57 years in a way that potentially affected juvenile salmon survival. Water temperature  
58 increased rapidly during the spring in the Connecticut River (Fig A1A). Across years,  
59 water temperature at any given site varied on any date (Fig A1A, A1B ), such that a smolt  
60 using a temperature cue to begin migration might begin at very different times in  
61 different years. While temperature generally increased from upstream to downstream on  
62 any given date (Fig A1B), there were many individual dates in individual years in which  
63 breaks from this pattern occurred, with irregular warm or cold spots occurring within the  
64 longitudinal temperature gradient.

65

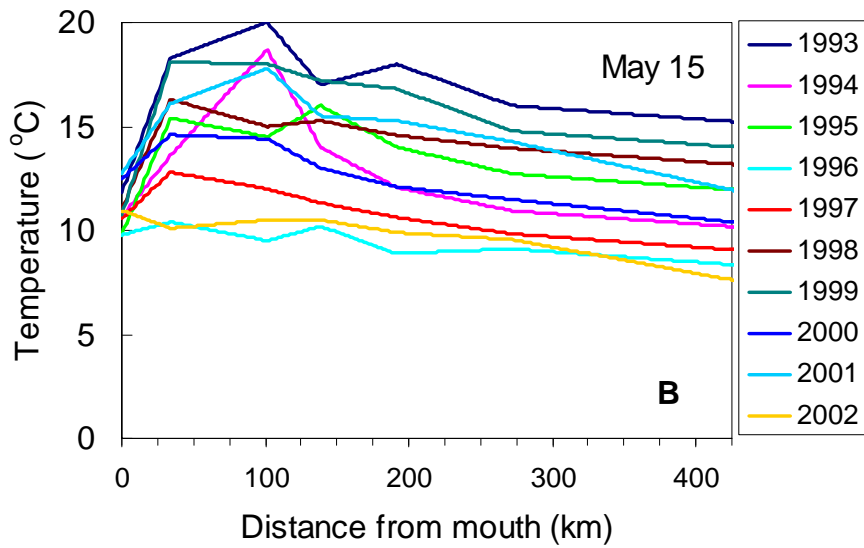
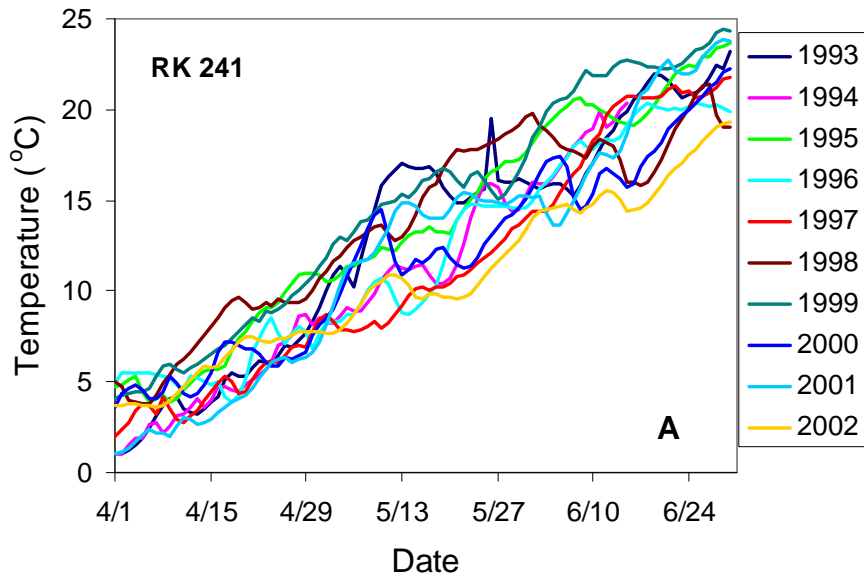
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67 Table A1. Conversion of discharge ( $x$ ,  $\text{ft}^3/\text{s}$ ) to velocity ( $y$ ,  $\text{cm}/\text{s}$ ) using discharge and  
68 cross-sectional area data from USGS Water Information System at 4 sites along the  
69 course of the Connecticut River, identified by river kilometer.

<b>RK</b>	<b>Conversion function</b>	<b><math>R^2</math></b>
428	$y = -2.83 \times 10^{-5} x^2 + 5.66x + 1.07 \times 10^4$	$R^2 = 0.935$
346	$y = -5.66 \times 10^{-5} x^2 + 5.66x + 6.31 \times 10^4$	$R^2 = 0.802$
191	$y = -8.51 \times 10^{-6} x^2 + 2.55x + 2.76 \times 10^4$	$R^2 = 0.916$
101	$y = -1.13 \times 10^{-5} x^2 + 2.83x + 1.03 \times 10^4$	$R^2 = 0.977$

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Figure A1. Example of Connecticut River water temperatures in years 1993-2002. A) Interpolated temperature data from RK 241 (near the inflow of the West River) from April 1 to June 30, the time period when Atlantic salmon smolts migrate from tributaries to the ocean. B) Interpolated temperature data for May 15 from RK 0 to RK 425.

78 **Appendix B**

79

80 Table B1. Tributaries from which simulated smolts originated, the distance upstream

81 from the mouth of the river (km), and the mean relative proportion of smolts originating

82 from each tributary, based on parr estimates the previous fall in each tributary

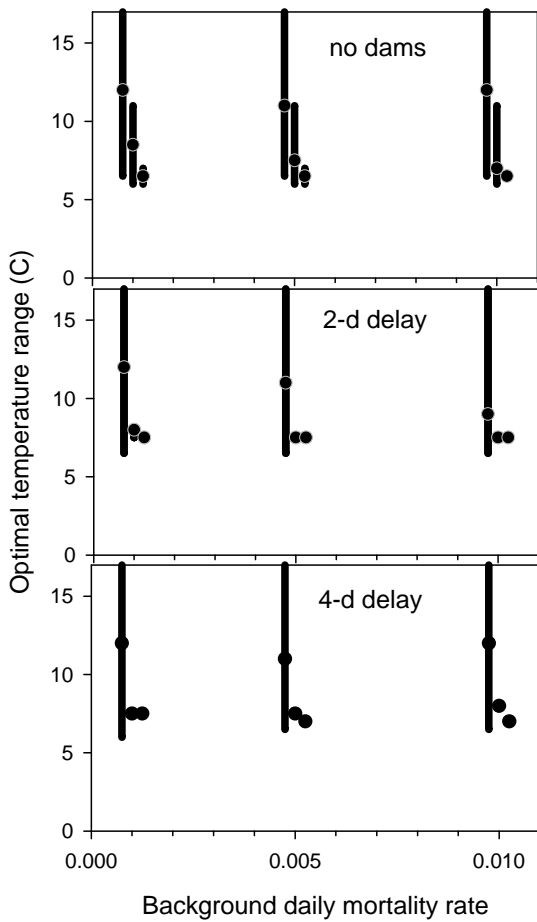
83 (Connecticut River Atlantic Salmon Commission Wild Smolt Estimates).

Tributary	RK	Relative
		Proportion
Wells River	428	0.03
White River	346	0.10
Williams River	286	0.09
West River	241	0.32
Deerfield River	190	0.13
Westfield River	125	0.17
Farmington River	93	0.12
Salmon River	29	0.04

84

85 **Appendix C**

86 Figure C1. Range of temperature cues yielding at least 75% total survival across all years  
87 (vertical bars) and absolute optimal temperature cue (circles) for smolts migrating from  
88 each of three tributaries, with no dams or 2 or 4 day delay at dams, at three levels of  
89 background mortality rate. Within each panel, within each mortality rate grouping, bars  
90 represent smolts from different tributaries, from left to right: Salmon River (RK 29),  
91 West River (RK 241), and Wells River RK (428). Circles with no bars indicate optimal  
92 temperature cues, but not cues that result in at least 75% survival.



93

94 **Appendix D**

95

96 Figure D1. Percent survival (mean  $\pm$  S.D.) of smolts from three tributaries (Wells, West,

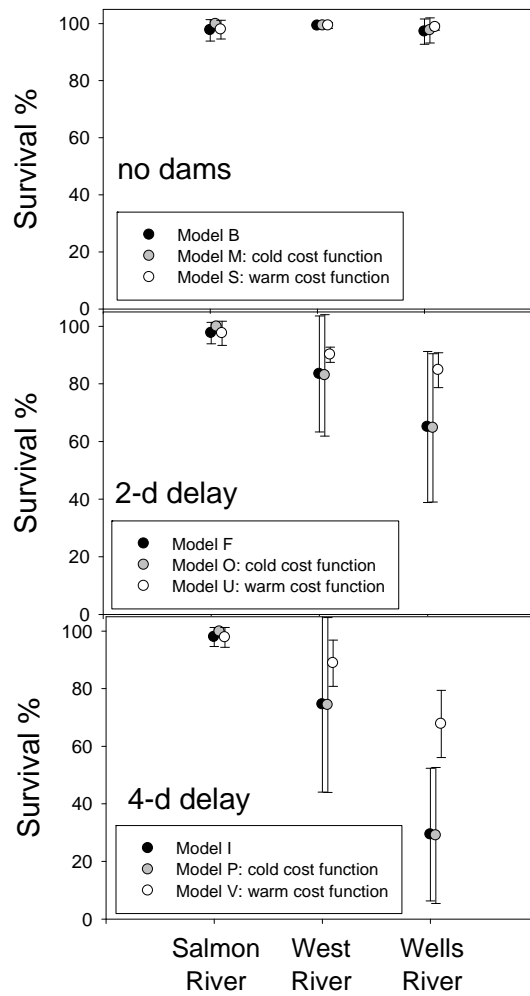
97 and Salmon rivers) in simulation with dams (panel A), with a 2-d delay at dams (panel

98 B), and with a 4-d delay at dams (panel C). Data are shown for the original temperature

99 cost functions (Models B, F, and I; black circles), the alternative cold-cost function

100 (Models M, O, and P; gray circles), and the alternative warm-cost function (Models S, U,

101 and V; white circles).



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