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3 **Evolutionary responses to climate change for organisms with**  
4 **complex life histories: Columbia River salmon as a case in point**  
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6 Running head: Evolutionary responses to climate change in salmon  
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**Abstract**

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Salmon life histories are finely tuned to local environmental conditions, which are intimately linked to climate. We summarize the likely impacts of climate change on the physical environment of salmon in the Pacific Northwest and discuss potential evolutionary consequences of these changes, with particular reference to Columbia River basin spring/summer Chinook (*Oncorhynchus tshawytscha*) and sockeye (*O. nerka*) salmon. We discuss possible evolutionary responses in migration and spawning timing, egg and juvenile growth and development rates, thermal tolerance, and disease resistance. We know little about ocean migration pathways so cannot confidently suggest potential changes in this life stage. Climate change might produce conflicting selection pressures in different life stages, which will interact with plastic (i.e., non-genetic) changes in various ways. To clarify these interactions, we present a conceptual model of how changing environmental conditions shift phenotypic optima and, through plastic responses, phenotype distributions, affecting the force of selection. Our predictions are tentative because we lack data on the strength of selection, heritability, and ecological and genetic linkages among many of the traits discussed here. Despite the challenges involved in experimental manipulation of species with complex life histories, such research is essential for full appreciation of the biological effects of climate change.

## 60 Introduction

61 Climate change is transforming the fitness landscapes of millions of species at a  
62 rapid rate, but we have little understanding of the evolutionary consequences.  
63 Evolutionary responses to climate change are important because non-genetic responses,  
64 such as shifts of range edges and plastic phenotypic change, might not be sufficient for  
65 the persistence of many populations (Sala et al. 2000; Thomas et al. 2004), and because  
66 strong selection can increase the risk of extinction in small populations (Bürger and  
67 Lynch 1995). Evolutionary responses seem likely because of the prevalence of spatial  
68 variation in physiological and behavioral traits that reflect past adaptation to local climate  
69 (Garland and Adolph 1991; Davis et al. 2005; Reusch and Wood 2007), and growing  
70 evidence of contemporary evolution in response to a variety of environmental  
71 disturbances (Stockwell et al. 2003). However, despite a few notable exceptions, genetic  
72 responses to climate change have proven difficult to demonstrate (see reviews in  
73 Bradshaw and Holzapfel 2006; Reusch and Wood 2007; Gienapp et al. 2008). Most  
74 phenotypic change recently observed might be largely due to plastic (i.e., non-genetic)  
75 change (Reale et al. 2003a; Berteaux et al. 2004; Gienapp et al. 2008). Persistence  
76 through climate change will continue to depend on plastic responses, because  
77 evolutionary responses are often limited and can impose demographic costs (Lynch and  
78 Lande 1993; Bürger and Lynch 1995). Furthermore, the distinction between genetic and  
79 plastic responses is simplistic because populations show genetic differences in their  
80 plasticity (i.e., different “norms of reaction”), and these can evolve (Nussey et al. 2005).  
81 Plastic and genetic mechanisms interact in complicated ways, and it is important to  
82 disentangle them in order to predict the effects of climate change on natural populations.

83 Most empirical research to date has considered evolutionary responses to  
84 environmental change in single traits, such as a shift in photoperiodic cues for diapause in  
85 mosquitoes (Bradshaw and Holzapfel 2006), dispersal ability in crickets (Thomas et al.  
86 2001) and butterflies (Hill et al. 1999), or chromosome inversion rates in *Drosophila*  
87 (Balanya et al. 2006). This single-trait approach yields insights, but selection is often  
88 more complicated. For example, in species with complex life histories, selection due to  
89 climate change can act simultaneously on multiple traits in ways that differ through the  
90 life cycle (Prout 1971; Lande and Arnold 1983; Arnold and Wade 1984; Lynch 1999).  
91 Changes in one life stage can have extensive repercussions for later life stages,  
92 particularly in migratory animals, where multiple life-stage transitions are finely tuned to  
93 conditions in radically different environments. Genetic covariances between traits under  
94 different selection pressures will shape the response to selection (Etterson and Shaw  
95 2001). Moreover, community interactions are likely to be disturbed, simply because  
96 phenological responses of interacting species might not be parallel (Harrington et al.  
97 1999; Visser and Both 2005).

98 We explore how these various mechanisms might interact to shape the selective  
99 environment in the case of Pacific salmon (*Oncorhynchus spp.*). Salmon species have  
100 plastic life histories, but adaptation of reaction norms to local environmental conditions at  
101 a very fine spatial scale (e.g., Tallman 1986; Quinn et al. 2000; Beer and Anderson 2001;  
102 Keefer et al. 2004) suggests that climate change will profoundly affect salmon life  
103 histories, and the interplay between genetic and plastic responses is likely to be  
104 important. The anadromous salmon life cycle depends crucially on appropriate timing of

105 transitions between habitats, so the potential for a growing mismatch between the needs  
106 of different stages in relation to these transitions is a major concern. Many salmon  
107 populations in the Pacific Northwest are already threatened with extinction, so the effects  
108 of climate on absolute fitness (i.e., a population's capacity for replacing itself) warrant  
109 conservation concern, and must be considered in the context of a web of natural and  
110 anthropogenic agents of selection (Waples et al. 2008).

111 A consequence of extensive local adaptation and life history diversity in salmon is  
112 that climate change will differ in its effects on specific populations; review of all these  
113 effects is beyond the scope of this paper. Rather, we emphasize the interacting and  
114 cumulative effects of climate change across the life cycle. To accomplish this, we focus  
115 on a particular set of Chinook (*O. tshawytscha*) and sockeye (*O. nerka*) populations  
116 having certain life history commonalities (namely, spring adult migration and yearling  
117 juvenile outmigration) within the Columbia River Basin. The Columbia River marks the  
118 southern limit of the geographic range of sockeye, but it is well within the range of  
119 Chinook salmon (Groot and Margolis 1991). Chinook salmon persist south of the  
120 Columbia River in Oregon and California and were abundant historically, but these  
121 populations are genetically and behaviorally very distinct from the populations  
122 considered here. Snake River spring/summer Chinook salmon that are our primary focus  
123 are the southernmost populations of a northern ecotype of Chinook, defined by a  
124 combination of juvenile seaward migration, ocean migration pattern, and the season of  
125 adult return (Taylor 1990; Healey 1991; Waples et al. 2004). We argue here that these  
126 characteristics will become increasingly maladapted with climate change. These  
127 populations are listed as threatened under the U.S. Endangered Species Act (NMFS  
128 1992), so any further decline in fitness significantly threatens their persistence (McClure  
129 et al. 2003; Crozier et al. 2008).

130 In the following sections, we first explain the complex nature of Pacific salmon  
131 life histories and their adaptations to diverse environments across the Pacific Rim. We  
132 then consider how these environments, particularly those experienced by our focal  
133 populations, are expected to change due to climate warming. We next examine evidence  
134 for local adaptation to climate, likely changes in selection with climate change, and  
135 potential evolutionary responses for certain traits during particular life stages. Finally,  
136 we discuss the importance of integrating potential plastic and evolutionary responses  
137 across multiple traits and life-history stages.

## 138 **Salmon life-history diversity**

139 Pacific salmon have complex life histories that span diverse environments across  
140 the Pacific Rim (Groot and Margolis 1991; Quinn 2005). They spawn in fall in fresh  
141 water and their embryos incubate in the gravel during the winter and emerge in spring.  
142 Juveniles then spend days to years in habitats ranging from small creeks to large rivers,  
143 and small ponds to large lakes. Most juveniles then migrate downriver, through estuaries  
144 and coastal waters, to the ocean. These "anadromous" individuals spend anywhere from a  
145 few months to as much as seven years at sea, before migrating back to spawn, and most  
146 die at their natal sites in fresh water. This great diversity of environments and behaviors  
147 suggests that climate change could influence selection on multiple traits in multiple  
148 phases of the life cycle.

149 Life-history diversity in salmon reflects a combination of phenotypic plasticity in  
150 response to variable environmental conditions (Hutchings 2004) and local adaptation  
151 throughout the life cycle, across the complete suite of life history, morphological,  
152 physiological, and behavioral traits (Ricker 1972; Groot and Margolis 1991; Taylor 1991;  
153 Quinn 2005). Phenotypic plasticity facilitates rapid colonization of new habitats and  
154 immediate responses to environmental change (Quinn et al. 2001; Price et al. 2003;  
155 Ghalambor et al. 2007). Local adaptation is facilitated by strong natal homing that limits  
156 gene flow between populations in different selective environments. Despite the  
157 remarkable extent of plasticity and local adaptation, appropriate and sufficient responses  
158 to climate change are not assured because of the uncertain rate and nature of climate  
159 change, the genetic properties of traits, the effects of invasive species and other stressors  
160 (e.g., hatcheries, fishing, hydroelectric dams).  
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## 162 **Expected climate change**

163 Projections for 21<sup>st</sup> century climate around the Pacific Rim and in the Pacific  
164 Ocean suggest significant surface warming trends, especially at higher latitudes and over  
165 continents. A range of models and greenhouse gas and aerosol emissions scenarios  
166 project global average warming from  $\sim+1$  to  $+6^{\circ}\text{C}$  by the year 2100 (IPCC 2007). For  
167 the Pacific Northwest (coastal North America from northern California to southern  
168 British Columbia, Fig. 1), warming is projected to be near the global average. Most  
169 climate models project modest increases in winter precipitation for this region (on  
170 average,  $\sim 10\%$ ), but projections for summer precipitation form no consistent pattern  
171 (Salathé 2006).

172 These climate-change projections indicate clear hydrologic changes for salmon-  
173 bearing streams in western North America. Winter will become milder, causing more  
174 precipitation to fall as rain and less as snow in locations where surface temperatures have  
175 historically been near freezing. A warming climate in the second half of the 20<sup>th</sup> century  
176 caused a significant advance in timing of snowmelt runoff for many rivers in the region  
177 (Stewart et al. 2005). Additional warming is expected to cause further shifts in the onset  
178 of snowmelt in streams that now carry a substantial snowpack into the spring and summer  
179 seasons. A warmer atmosphere has a higher capacity for water vapor, which promotes  
180 greater hydrologic extremes: more severe drought in summer and more intense  
181 precipitation and flooding in winter. Rising surface air temperatures will also cause  
182 stream and estuary temperatures to rise. Over the North Pacific Ocean, important  
183 changes in salmon habitat will depend primarily on 1) rising upper ocean temperatures  
184 that increase the stratification of the upper ocean, 2) changes in surface wind patterns,  
185 potentially changing the timing and intensity of the upwelling of nutrient-rich subsurface  
186 water, and 3) increasing ocean acidification changing plankton community composition  
187 with effects cascading through marine food-webs.

188 This is the template of climate change that is expected to influence the evolution  
189 of Pacific salmon in the 21<sup>st</sup> century. We now explore the evolutionary implications of  
190 these trends for the phenology of critical periods in the life history of salmon. For each  
191 trait, we (1) describe how climate change might alter the selective regime, (2) review the  
192 trait's genetic variation and heritability ( $h^2$ ), and (3) assess the likelihood and relative  
193 speed of potential evolutionary responses. It is important to remember that the following

194 conclusions are merely hypotheses, in part because few studies have formally measured  
195 selection on salmon in response to environmental change. We do cite those studies but  
196 more are certainly needed.  
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## 198 **Potential evolutionary pressures and responses**

### 199 **Heat tolerance**

200 The most obvious effect of climate change will be higher temperatures in fresh  
201 water. Warmer water can accelerate growth and development where temperatures are  
202 below optimal, or stress fish if they cannot behaviorally avoid temperatures that are  
203 above optimal. Fitness in warm water is reduced by mortality at lethal temperatures, and  
204 various impacts at sublethal temperatures, such as increased susceptibility to warm-water  
205 diseases, inhibition of normal behavior, growth and development, especially  
206 smoltification, maturation, and egg development, and increased energetic costs (for  
207 reviews, see McCullough 1999; Materna 2001). Despite the high elevation at which most  
208 of the populations considered here spawn and rear, much of the rearing habitat already  
209 exceeds optimal temperatures for salmonids at times (Donato 2002). Temperatures  
210 approach lethal limits in the mainstem Columbia, Snake, and Okanagan Rivers regularly,  
211 affecting the times fish can migrate to and from the ocean (Hodgson and Quinn 2002;  
212 Hyatt et al. 2003; Brannon et al. 2004; Naughton et al. 2005).

213 Variation in temperature-specific survival rates occurs among populations from  
214 different thermal regimes, suggesting that thermal tolerance can evolve in the wild. For  
215 example, coastal Chinook salmon populations show lower egg and embryo survival and  
216 lower yolk conversion efficiency at cold temperatures than do interior populations  
217 (Beacham and Murray 1989), and juvenile Chinook salmon from southern British  
218 Columbia tolerate longer exposure to high temperatures than those from northern British  
219 Columbia (Beacham and Withler 1991). Beacham and Withler (1991) found heritability  
220 for heat tolerance to be significant in the population from the cooler stream ( $h^2=0.27$ ), but  
221 not in the population from the warmer stream ( $h^2=0.00$ ), suggesting that selection had  
222 acted in the latter population to increase heat resistance. Nonetheless, differences in  
223 upper lethal temperatures between populations from very different thermal environments  
224 are subtle and sometimes disappear with appropriate acclimation and testing (e.g., Brett  
225 1956; Konecki et al. 1995b; Konecki et al. 1995a). Overall, these and other studies  
226 suggest a potential for local adaptation of heat tolerance, but the limitation of salmon to  
227 habitat below  $\sim 23^\circ\text{C}$  (McCullough 1999) points to an ultimate upper limit to heat  
228 tolerance that evolution cannot surmount.

229 Populations near this upper thermal limit seem to persist through behaviors that  
230 reduce exposure to the highest temperatures, such as the occupation of cold-water refugia  
231 (Berman and Quinn 1991; Torgersen et al. 1999; Goniea et al. 2006). From the  
232 perspective of climate-induced warming, it would be valuable to know whether  
233 populations differ genetically in their tendency to adopt these behaviors. If all  
234 populations harbor the potential for behavioral avoidance of warm water, then these  
235 responses might ameliorate some of the effects of climate change except in sites lacking  
236 thermal refuges. If not, use of such refuges might depend on evolution of appropriate  
237 behaviors, and the potential for this is entirely unknown.

238

**239 Disease resistance**

240 Many parasitic and bacterial diseases infect salmon, and some of these infections  
241 become more virulent with increasing temperature (McCullough 1999). Reasons for this  
242 include lower host resistance when the fish are thermally stressed, and higher pathogen  
243 population growth rates, due to shorter generation times at higher temperatures  
244 (Marcogliese 2001). Diseases of wild salmon likely to become a greater problem with  
245 warmer temperatures include those caused by the myxosporidian parasite *Ceratomyxa*  
246 *shasta*, the bacterium *Flexibacter columnaris*, and by various *Aeromonas* and *Listonella*  
247 species (McCullough 1999). These pathogens are ubiquitous and infection rates can be  
248 very high (Ordal and Pacha 1963; Chapman 1986; Tiffan et al. 1996). As the availability  
249 of cool water decreases, mortality rates will likely increase and selection should favor  
250 increased resistance to these diseases.

251 Salmon populations that have been exposed to particular diseases historically tend  
252 to have higher resistance to those diseases (Zinn et al. 1977; Bower et al. 1995;  
253 Bartholomew 1998; Miller and Vincent 2008). The Columbia River has already  
254 undergone changes (increased temperature, lower flows, slower juvenile migration) that  
255 probably have increased exposure and susceptibility to certain diseases. Ordal and Pacha  
256 (1963) identified high *columnaris* infection rates as a potential cause for the decline of  
257 Columbia River Chinook, sockeye and steelhead trout in the early 1960s. Although  
258 experiments are complicated by enormous variability in strain virulence, it would be  
259 informative to see if resistance has increased compared with their findings, and those of  
260 Zinn et al. (1977).

261 The rate at which resistance responds to changes in pathogen prevalence or  
262 virulence will depend in part on its heritability. Heritabilities for resistance to common  
263 diseases range from very low to moderate, but tend to be lower in populations that have  
264 historically been exposed to the disease (0 to 0.34, Beacham and Evelyn 1992; 0.13 Hard  
265 et al. 2006). Low heritabilities will limit the pace of future adaptation in populations that  
266 already show some resistance, such as our focal populations.

**267 Upstream migration**

268 Snake River spring/summer Chinook salmon spawn in the Salmon River basin in  
269 central Idaho, at the highest elevations of any salmon population (up to 2000 m above sea  
270 level, Fig. 1). They also complete some of the longest migrations: up to 1500 km from  
271 the ocean to their spawning sites. Columbia River sockeye salmon migrate up to 1000  
272 km to spawning grounds in the Wenatchee and Osoyoos lakes. Successful spawning in  
273 such populations requires that they (1) stay in the ocean long enough to acquire adequate  
274 energy stores, (2) use energy efficiently during migration, (3) avoid migration when  
275 conditions are especially difficult (e.g., high temperatures, very low flow), and 4) arrive  
276 prior to the appropriate spawning date. Climate change will likely alter the optimal  
277 balance between these demands owing to changes in temperature and flow that influence  
278 mortality and energy costs (Hinch and Rand 1998; Rand et al. 2006; Young et al. 2006).

279 Most fish in our focal populations migrate up the Columbia River in April and  
280 May, prior to peak temperatures, and then hold in deep, cool pools before moving to  
281 spawning grounds. Snake River Chinook salmon spawn in mid- to late-August (Good et

282 al. 2005), and Columbia River sockeye salmon spawn in October (Hyatt et al. 2003).  
283 Migration prior to peak temperatures is presumably necessary in order to complete their  
284 long migration prior to the appropriate time for spawning. Late migrants have high  
285 mortality during the migration (Naughton et al. 2005) or experience delays while they  
286 seek thermal refugia (High et al. 2006; Salinger and Anderson 2006), probably owing to  
287 the warmer water in July and August. Mean July water temperature in the Columbia  
288 River has risen steadily from 16.9°C in 1950 to 20.9°C in 2006 (measured at Bonneville  
289 Dam, Fig. 3, DART 2007). Not only are peak temperatures warmer, but high  
290 temperatures last longer; compared to the late 1930s, stressful temperatures now begin a  
291 full month earlier and persist 2-3 weeks later (Quinn and Adams 1996). In short, recent  
292 selection against migration during stressful summer temperatures has likely favored  
293 earlier migration in spring.

294 Consistent with this prediction, a trend toward increasingly earlier migration over  
295 the past century in spring/summer Chinook and sockeye (*O. nerka*) salmon is evident  
296 (Fig. 3, and Quinn and Adams 1996). However, the extent to which these responses are  
297 plastic or genetic is unclear, and might be confounded with changing abundance of  
298 populations that differ in timing, or by changes in hatchery production or harvest. Sea  
299 surface temperatures can influence migration timing via plasticity, but this effect tends to  
300 be weak (Hodgson and Quinn 2002; Hodgson et al. 2006). Furthermore, the high  
301 heritability of timing-related traits (median 0.51 Carlson and Seamons 2008) supports the  
302 plausibility of evolutionary adaptation due to strong selection resulting from changing  
303 conditions.

304 Compared with spring Chinook salmon, Columbia River basin sockeye are more  
305 suitable for exploring the probable strength of the selection differential caused by rising  
306 temperatures because their simpler population structure and minimum of hatchery  
307 propagation simplify analysis of time trends (Quinn and Adams 1996; Hodgson et al.  
308 2006). Here, earlier migration appears to have evolved owing to warming water  
309 conditions in the Columbia River (Quinn and Adams 1996). Recent analyses (L. Crozier,  
310 unpubl. data) support this conclusion by quantifying thermal selection for earlier  
311 migration over the past 50 years. Specifically, sockeye salmon that survive migration are  
312 expected to pass Bonneville Dam on average 2.5 days earlier per generation (0.3 standard  
313 deviations) than the population average, based on a probabilistic model of temperature-  
314 induced mortality, and historical records of migration time and temperature. With this  
315 selection differential, the observed shift in migration timing of 8.6 days (Fig. 3) could be  
316 accomplished with a migration timing heritability of only 0.24. This value is certainly  
317 plausible (cf 1.06 Quinn et al. 2000), indicating that evolutionary change could easily  
318 account for the observed trend in migration timing. Even so, the future evolution of  
319 migration time will eventually be constrained by eroding genetic variation and conflicting  
320 demands. For example, if salmon migrate earlier in the summer but spawn at the same  
321 date in fall (or even later), they will need more energy to sustain themselves for the  
322 longer period of fasting. This need for more stored energy might be in conflict with the  
323 need to leave the ocean earlier in the summer, missing some of the best growing  
324 conditions.



**325                    Spawning date, emergence timing, and development rates**

326                    Snake River spring Chinook salmon spawn in the late summer; embryos develop  
327 over winter and emerge from the gravel as fry in early spring. In general, emergence  
328 timing appears to be under stabilizing selection, because fry have low survival if they  
329 emerge too early, before food is seasonally available, or too late to capitalize on crucial  
330 growth opportunities (Brannon 1987; Einum and Fleming 2000; Letcher et al. 2004).  
331 Embryo development rates are tightly linked to water temperature (Beacham and Murray  
332 1990), so optimal emergence timing must match local conditions through adjustments to  
333 spawning date or genetically-based, temperature-specific embryo development rates  
334 (Brannon 1987; Brannon et al. 2004). Indeed, even small differences in water  
335 temperature among nearby spawning locations can influence spawning date (Beer and  
336 Anderson 2001). On the other hand, spawning date can sometimes vary for reasons other  
337 than selection on emergence timing, such as habitat inaccessibility at a particular time or  
338 energetic demands on adults, and in such cases temperature-specific development rates  
339 might evolve (Tallman 1986; Tallman and Healey 1991).

340                    Warmer winters will accelerate development and lead to earlier emergence. The  
341 optimal time for emergence will also advance, because seasonal initiation of primary and  
342 secondary productivity in general is temperature-sensitive. However, fry emergence and  
343 optimal food conditions might not advance at the same rate. If emergence timing  
344 diverges from optimal conditions, then selection should favor compensatory changes in  
345 spawning date or temperature-specific development rates. Spawning date is particularly  
346 likely to evolve owing to its high heritability in salmonids (Quinn et al. 2000; Hard 2004;  
347 Hendry and Day 2005; Carlson and Seamons 2008). In fact, spawning date has evolved  
348 quickly in populations transplanted to new environments. Chinook salmon populations  
349 transplanted to New Zealand, for example, have diverged several weeks in maturation  
350 date, which is closely related to spawn time, in the 80 years since their introduction  
351 (Quinn et al. 2000; Unwin et al. 2000; Quinn et al. 2001). Moreover, this evolutionary  
352 divergence matches expectations: later spawning occurs in the populations where  
353 embryos develop in warmer water. Spawning date in Columbia River salmon thus might  
354 evolve rapidly in response to climate change, unless artificial propagation of the  
355 population exerts countervailing selection (Quinn et al. 2002).

356                    It is less certain whether temperature-specific development rates will evolve with  
357 climate warming. Although development rates do seem adapted in some situations to  
358 match emergence timing to favorable conditions, the most dramatic variation is among  
359 groups that spawn at different times in the same site (Tallman 1986; Brannon 1987;  
360 Tallman and Healey 1991; Hendry et al. 1998). Moreover, the heritability of embryo  
361 development rate seems much lower (Hebert et al. 1998; Kinnison et al. 1998) than that  
362 for spawning date, suggesting that evolution of development rates will be relatively slow.  
363 Consistent with this expectation, the divergence in spawning date among New Zealand  
364 Chinook salmon populations was not accompanied by divergence in temperature-specific  
365 development rates (Kinnison et al. 1998; Unwin et al. 2000). However, if changes in  
366 spawning date do not lead to optimal emergence timing, changing development rates  
367 would be the only evolutionarily mechanism to adjust emergence timing.

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### **Juvenile rearing**

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After the fry in our focal populations emerge from the gravel, they spend a year in the stream (in the case of the Chinook salmon) or lake (sockeye) before migrating to the ocean. For sockeye salmon, growth in some streams is higher under warmer conditions (Schindler et al. 2005), although complex phenological changes may not always benefit sockeye fry (Hampton et al. 2006). For Chinook salmon, survival during this period is lower under warmer and lower-flow conditions (Crozier and Zabel 2006), which could increase the risk of extinction by 29-86% (Crozier et al. 2008). Potential evolutionary responses will depend on the mechanisms by which low fall flows and high summer temperatures reduce survival. Likely candidates include influences on growth rates and predation. Little is known about the evolutionary responses of juvenile salmon to changes in predation, so we here focus on growth.

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Local adaptation of growth rate to water temperature does occur in at least some salmonines (Jensen et al. 2000; Finstad et al. 2004), notably after introduction to new environments (Haugen and Vollestad 2000; Quinn et al. 2001). Moreover, the contributions of body size and growth rate to survival in salmonids do appear to vary with environmental conditions (Zabel and Williams 2002; Zabel and Achord 2004). Although these patterns suggest growth rates can evolve in response to changing temperatures, there are several reasons for caution. First, the heritability of growth rate can be relatively low (0.04-0.3) in wild Chinook salmon (Hard 2004; de Leaniz et al. 2007; Carlson and Seamons 2008; Waples et al. 2008). Second, evolutionary responses are difficult to predict because growth rates are genetically correlated with many other traits under selection, such as egg size, agonistic behavior, age and size of smolting, and age and size at maturity (Hard 2004). Third, adaptation of growth rates to local temperatures appears strongest at low, rather than high, temperatures (Jensen et al. 2000). Finally, studies formally estimating natural selection in salmonid populations experiencing environmental change have not found strong selection on growth rate or body size (Hendry et al. 2003; Carlson et al. 2004). We tentatively conclude that climate-induced changes in growth rate are likely to be primarily plastic.

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### **Downstream migration and early ocean stages**

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The periods of downstream migration and ocean entry are especially hazardous for salmon. Although many traits can influence survival during these periods, we focus on migration timing, which has been well studied and shows the potential for both plastic and genetic responses to climate change. The optimal timing of downstream migration, like that of upstream migration, reflects a trade-off between the time for growth before migration and the hazards of seasonally deteriorating river or ocean conditions. Smolt migration timing varies among populations (Peven 1987; Healey 1991; Orciari and Leonard 1996; Achord et al. 2001), but the relative contribution of genetic differences versus phenotypic plasticity to these patterns remains uncertain.

For our focal Chinook populations, survival during downstream migration is negatively correlated with temperatures over 13°C and positively correlated with flow (Achord et al. 2007). An earlier snowmelt and rising summer temperatures will cause unfavorable river conditions to occur earlier in summer, thus potentially favoring earlier

412 migration. At present, salmon seem to be responding plastically by migrating earlier in  
413 years with warmer fall and spring temperatures (Achord et al. 2007), consistent with  
414 patterns seen in these species elsewhere (Quinn 2005). Phenotypic plasticity might thus  
415 accommodate climate change. However, with climate change, changes in conditions at  
416 the rearing location might not exactly parallel changes in conditions in the lower river,  
417 estuary, and coastal environments. That is, earlier migration might well be adaptive with  
418 respect to survival in the upper river but not with respect to survival in the lower river or  
419 ocean. In such cases, the plastic response might not be adaptive and selection might  
420 favor a genetically-based response. No studies have yet documented genetically-based  
421 changes in smolt migration timing, but the trait appears to have a genetic basis (Stewart et  
422 al. 2006, and references therein).

423 Factors influencing the optimal timing of ocean entry are more difficult to predict  
424 but clearly important. Survival over the entire period of ocean residency is usually <4%  
425 for Snake River Chinook salmon (Williams et al. 2005), and most mortality is thought to  
426 occur within weeks to months of ocean entry (Pearcy 1992). Survival probabilities  
427 during this period are related to ocean conditions when the juveniles arrive (Logerwell et  
428 al. 2003; Scheuerell and Williams 2005; Zabel et al. 2006). Salmon grow quickly when  
429 upwelling winds bring cool, nutrient-rich, water to the surface, stimulating the growth of  
430 plankton. Cooler water also reduces predation by displacing warm-water predators  
431 offshore. Some models predict that climate change will increase the intensity of  
432 upwelling but delay its onset (Snyder et al. 2003; Diffenbaugh et al. 2004). At present,  
433 naturally migrating smolts with earlier ocean entry usually have higher ocean survival,  
434 possibly reflecting maladaptation introduced by the effects of dams on migration speed  
435 (Zabel and Williams 2002; Waples et al. 2008). A delay in upwelling might improve  
436 survival of late-entry smolts, ultimately selecting for later ocean entry. Later initiation of  
437 smolt migration or slower migration through the river would likely increase in-river  
438 mortality, thus setting the stage for climate change to impose contradictory selection on  
439 migration timing through in-river survival (favors earlier migration) and early-ocean  
440 survival (favors later migration). Other climate models predict that upwelling will instead  
441 shift earlier in the season (Hsieh and Boer 1992), in which case the two aspects of  
442 selection are instead complementary.

443 In this discussion we have assumed that river conditions affect migration survival,  
444 and that arrival time in the estuary depends directly on migration date. At present the  
445 vast majority of smolts (>80%) are, however, collected at up-stream dams and taken  
446 downriver in barges. These fish can reach the estuary in 2 days instead of 2-6 weeks.  
447 Although earlier ocean-entry in general appears advantageous for this population, barged  
448 fish typically have lower adult return rates than naturally migrating fish (Williams et al.  
449 2005). The reasons for this difference are controversial (Budy et al. 2002; Muir et al.  
450 2006). But regardless of the reasons, human actions have such a major impact on the  
451 selection pressures these fish experience, it is misleading to consider potential  
452 evolutionary responses to climate change without considering our role (Waples et al.  
453 2008).

454

### **Ocean residence**

455 Most Columbia River salmon spend 1 to 4 years in the ocean, depending on  
456 environmental and genetic factors, so ocean conditions undoubtedly also impose

457 selection. Ocean growth rates will likely respond to climate change through alterations in  
458 metabolic costs of foraging in a warmer ocean and shifts in prey abundance, composition,  
459 and distribution. We do not know enough either about how ocean food webs will  
460 respond to climate change or how Chinook or sockeye salmon will respond to these  
461 changes to predict specific evolutionary consequences. Genetic variability in the  
462 migration patterns of salmon (Pascual and Quinn 1994; Kallio-Nyberg et al. 2000)  
463 represents potential for adaptation of migration routes toward regions favorable for  
464 growth and survival. However, these processes are so poorly understood that it is  
465 difficult to speculate how rapidly adaptation might occur, and how it would interact with  
466 proximate responses to currents, temperature, food availability and other stimuli.

## 467 **Integrating across the complexity**

468 In outlining the above suite of traits and life stages, we have attempted to assess  
469 how climate change might alter natural selection and drive evolutionary responses in a  
470 particular set of salmon populations (Table 1). We have highlighted interesting aspects  
471 of specific traits but have not considered interactions among them in detail. We now  
472 begin to address this complexity by proposing a conceptual model that integrates climate,  
473 plastic, and evolutionary effects across a particular life-history type, yearling juvenile and  
474 spring/summer adult migrating salmon. We focus on the timing of life-history events  
475 because phenology is likely to respond to climate change both evolutionarily and through  
476 plasticity (Bradshaw and Holzapfel 2008), and because changes in phenology at one life  
477 stage can directly affect phenology at other stages. We consider the timing of four major  
478 life-history events: upriver migration, spawning, emergence from the gravel, and smolt  
479 migration. Note that we do not expect the following analysis to be correct in all respects,  
480 or to apply to all populations. Rather, we outline possibilities and a framework as a basis  
481 for an integrated discussion.

482 We start by assuming (Fig. 4, top panel) that in a population, the peak of the  
483 phenotype distribution of timing (solid) for each life-history event coincides with the  
484 peak of the fitness function for that event (height of the dotted curve indicates the  
485 expected fitness of an individual with that timing phenotype). We therefore assume that  
486 salmon populations are locally adapted before climate change, such that the mean timing  
487 of each event approximates the optimal timing. It is certainly possible that the current  
488 populations are not adapted for the current conditions, given that the Columbia River has  
489 changed so dramatically and hatchery propagation and fisheries can exert countervailing  
490 selection. But attempting to integrate this possibility would mainly serve to complicate  
491 our illustration, and is better left for a subsequent analysis.

492 The second panel of Figure 4 represents how fitness functions might shift in  
493 position under one potential climate-change scenario. First, an earlier onset of stressful  
494 temperatures will select for earlier adult upstream migration (note, however, that  
495 populations tending to migrate after peak temperatures would be predicted to  
496 progressively migrate later under warming conditions). Second, optimal spawning date  
497 will shift later in the year because warmer water will otherwise hasten egg development  
498 and cause the fry to emerge too early. Earlier adult migration but later spawning implies  
499 a longer stay in freshwater, which imposes energetic costs and higher risk of predation  
500 and thermal stress. For later spawning to be favored, the costs imposed on juvenile  
501 survival from early emergence must outweigh the costs imposed on adult survival and

502 egg size. The actual shift in optimal spawning date will depend on the degree to which  
503 warmer water accelerates development more than it advances optimal emergence time,  
504 and the possibility of plastic response in spawning date, that might be greater in this  
505 population than generally reported in the literature (Dan Isaac, pers. comm.). Third,  
506 optimal emergence timing should be earlier because warmer water should advance the  
507 date at which food becomes available. Fourth, excessively high river temperatures during  
508 the summer will select for earlier migration of smolts, unless fifth, delayed upwelling  
509 along the coast favors postponement. This combination illustrates a potential conflict  
510 between selection on life stages in different habitats: warm river temperatures will select  
511 for earlier migration, but ocean conditions might favor later migration.

512 The third panel shows the expected plastic response of each life-history event to  
513 climate change. We first expect migration and spawning date to remain largely  
514 unchanged owing to their low plasticity. We next expect earlier emergence timing  
515 because warmer incubation temperatures accelerate development (again note that the  
516 actual shift depends on any change in spawning date). Similarly, we expect earlier  
517 downstream migration timing because on an annual basis, smolting is advanced by earlier  
518 warming. Ocean entry is likely to advance because migration speeds typically accelerate  
519 in warmer water.

520 The fourth panel shows potential natural selection on the timing of each life-  
521 history event as a result of the mismatch between the new optimum and the phenotype  
522 distribution. First, we expect selection for earlier migration and later spawning because  
523 the optima shift with climate change, but the traits do not shift plastically. We next  
524 expect little selection on emergence or downstream migration timing because, although  
525 the optimum has advanced, the plastic response is in that direction. Finally, selection on  
526 ocean entry timing might be strong because the plastic shift in migration timing acted in  
527 the opposite direction from the optimal.

528 This heuristic analysis illustrates the need for a closer examination of several key  
529 traits and stages. For example, selection on spawning date depends on at least three  
530 changes that are uncertain: (1) the advance in optimal emergence timing, (2) a plastic  
531 change in spawning date owing to warmer waters, and (3) potential costs of longer delays  
532 between migration and spawning. With regard to this last effect, advancing upstream  
533 migration dates and higher summer temperatures increase the length of time in freshwater  
534 during which energy stores are depleted, and cool-water refugia might contract,  
535 increasing pre-spawning mortality. This means that selection might not favor a delay in  
536 spawning date, which could then impose selection on embryo development rates for a  
537 given temperature. The lower heritabilities of embryo development rates would likely  
538 limit selection response. As another example, consistent delays in the onset of upwelling  
539 would select very strongly to delay the time of ocean entry. Accordingly, selection might  
540 favor delayed onset of smolt migration or a slower migration, and yet both of these  
541 effects seem unlikely given that high summer temperatures during migration increase  
542 mortality rates. Under these conditions, selection might favor direct adaptations to resist  
543 the stresses associated with high temperatures or early ocean entry. Note that changes in  
544 upwelling timing are very uncertain, so this is not the only plausible scenario.  
545 Nonetheless, it does draw attention to a particular case where the plastic response in one  
546 stage may be unfavorable for the subsequent life stage.  
547

## 548 **Conclusions**

549           Considerable uncertainty attends the prediction of evolutionary responses to  
550 climate warming (Holt 1990), even for a short-lived organism with a simple life cycle  
551 that is amenable to experiment (Etterson and Shaw 2001). The uncertainties are  
552 considerably greater for organisms like salmon that have complex, migratory life cycles.  
553 Selection pressures might differ greatly in different life stages, and appropriate  
554 phenological cues are critical for successful transitions between habitats. For salmon,  
555 like most organisms, both plastic and evolutionary mechanisms will contribute to  
556 phenological changes. Moreover, the persistence of individual salmon populations  
557 through climate change will likely depend on evolution of a variety of other, non-  
558 phenological traits as well.

559           We identified several traits with relatively high heritabilities, such as upstream  
560 migration date and spawning date, where we expect climate change to induce strong  
561 selection. Evolutionary responses in these traits are likely, as has been shown for other  
562 cases of environmental change influencing salmon (Hendry et al. 1998; Kinnison et al.  
563 1998; Hendry et al. 2000; Quinn et al. 2000; Quinn et al. 2001; Kinnison et al. 2008) and  
564 for other organisms (reviews: Hendry and Kinnison 1999; Reznick and Ghalambor 2001).  
565 We identified other traits, such as emergence timing, smolt migration timing, and habitat  
566 choice, where phenotypic change might largely reflect plasticity. These plastic responses  
567 might often be adaptive and should greatly reduce mortality compared with selection  
568 acting on the same traits (Price et al. 2003; Ghalambor et al. 2007). However, more work  
569 is needed to assess how plasticity and evolutionary changes feed back to affect the  
570 productivity and persistence of populations (Kinnison and Hairston Jr 2007; Kinnison et  
571 al. 2008).

572           Phenological changes are likely to be particularly important (see also Bradshaw  
573 and Holzapfel 2008). Indeed, some of the best evidence for phenotypic responses to  
574 environmental change are in the timing of migration or reproduction for salmon (Fig. 3;  
575 Quinn and Adams 1996) and for other organisms (Parmesan and Yohe 2003; Reale et al.  
576 2003b; Parmesan 2006). Most of this evidence is currently observational, so it remains  
577 difficult to assess the relative contributions of genetic change versus plasticity (Gienapp  
578 et al. 2008). We argue that these contributions are likely to differ among various timing  
579 events, as has been observed for some birds (Both and Visser 2005). In salmon, changes  
580 in juvenile migration timing are likely to be mostly plastic, whereas changes in adult  
581 migration timing are likely to be mostly genetic. The norm of reaction that governs  
582 juvenile migration time might evolve over time, especially in response to changes in  
583 climate variability, but we do not yet have enough information to predict this process.

584           Although strong phenological responses to climate change are likely, they are not  
585 without constraint and might not obviate selection on other traits. For example, the life-  
586 history of salmon balances the timing of numerous events during transit from headwaters  
587 to the ocean and back again. Change in one aspect of timing might thus directly affect  
588 subsequent life-history stages, perhaps in maladaptive ways. If so, phenological changes  
589 might not sufficiently balance environmental changes, and selection might occur on other  
590 traits, such as disease resistance, metabolic responses to temperature, and the sensitivity  
591 of developmental processes to temperature. These traits often show less heritability, so  
592 evolutionary change will be slower. In general, changes in one trait, which might be

593 plastic or genetic, will influence selection and evolutionary responses for other traits  
594 (Both and Visser 2001; Price et al. 2003; Ghalambor et al. 2007).

595 An important point to keep in mind is that *in situ* evolutionary change, while  
596 potentially saving distinctive populations from extirpation, might alter them so that they  
597 are no longer so distinctive. For example, Williams *et al.* (2008) argue that threatened  
598 Snake River fall Chinook salmon might be adapting to anthropogenic changes to their  
599 habitat by shifting from migration as sub-yearlings to migration as yearlings, thus  
600 gradually eliminating one of the dominant characteristics of the historical population.  
601 Ultimately, climate change might favor a change in the juvenile and adult migration  
602 phenology of Snake River spring/summer Chinook to the point that they no longer  
603 exhibit the northern ecotype of Chinook (Taylor 1990; Healey 1991; Brannon et al.  
604 2004). Currently, fall Chinook salmon (with the typically southern ecotype) spawn in the  
605 lower Salmon River (StreamNet 2005); with climate change, some aspects of this  
606 phenotype might become more suitable at higher elevations, eventually encroaching on  
607 the habitat currently occupied by summer Chinook salmon. If genetic variation in the  
608 existing population is low, or immigration high, trait replacement might occur through  
609 gene flow rather than evolution in isolation, reducing the genetic distinctiveness of this  
610 population complex (Waples et al. 2004). Indeed, replacement by gene flow appears to  
611 have occurred in some populations of mice experiencing environmental change (Pergams  
612 and Lacy 2008). Such a scenario is complicated by the different spawning habitat  
613 preferences and ocean migration patterns of the two phenotypes, which might be tied to  
614 juvenile or adult migration timing. The linkages between and constraints on all these  
615 traits are not fully understood. Nonetheless, whether through *in situ* change or gene flow,  
616 evolutionary change induced by climate change might dramatically alter the structure and  
617 integrity of the evolutionarily significant units on which conservation designations are  
618 based.

619 How representative is our case study? The great diversity of salmon life histories  
620 precludes extending the details of our analysis too broadly. For example, some  
621 populations have a short freshwater residency but a long estuarine residency, which  
622 should shift the stage and environment where climate change is most likely to alter  
623 selection pressures. Furthermore, particular climate impacts not considered here will also  
624 have a profound impact on the evolution and long-term survival of Pacific salmon  
625 populations. For instance, winter flooding strongly influences egg survival (Schuett-  
626 Hames et al. 2000; Seiler et al. 2002; Seiler et al. 2003), and is likely to increase  
627 extinction risk for some populations under climate change (Battin et al. 2007; ISAB  
628 2007). Sea level rise, ocean acidification, changes in stream productivity, increased  
629 habitat availability at the northern end of the range, and myriad other anticipated and  
630 unanticipated effects of climate change will further complicate the evolutionary puzzle  
631 confronting salmon.

632 Regardless of the specific selective factors that will most affect a particular  
633 population, salmon in general will respond to climate change with a dynamic tension  
634 between phenological and non-phenological change, as well as interacting plastic and  
635 genetic shifts in phenotypes. These are the fundamental processes that require focused  
636 study in near future. Integrated analyses have been useful in the study of squirrels (Reale  
637 et al. 2003a; Reale et al. 2003b) and migratory birds (Both and Visser 2001; Both and  
638 Visser 2005; Nussey et al. 2005; Both and Marvelde 2007), and are likely to prove

639 equally fruitful for salmon. Studies in wild salmon, in particular, are clearly needed,  
640 because most of the available genetic research has been conducted on hatchery fish  
641 (Carlson and Seamons 2008). Finally, because of the multiplicative impact of selection  
642 over the life cycle, it is crucial to consider the entire life cycle for species whose viability  
643 is at stake. A better understanding of the range of possible evolutionary responses to  
644 climate change is an essential component of effective, flexible strategies for the  
645 conservation of organisms with complex life histories, like salmon.  
646



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Table 1. Overview of some of the possible effects of climate change and potential plastic and evolutionary responses in Snake River spring/summer Chinook salmon. References with an \* are specific to this population.

Climate change effect	Confidence in physical effect	Effect on fish	Plastic response	Potential evolutionary response	Reference	
↑ peak summer and fall temperatures	high	↓ parr survival	seek cooler refugia		(Bisson and Davis 1976; McCullough 1999; Crozier and Zabel 2006*)	
		↑ or ↓ growth, depending on food supply and fish density		↑ energetic efficiency at high temperatures	(Brett et al. 1982; ISAB 2007)	
		↑ predation on juveniles	predator avoidance behavior, choosing suboptimal habitat			(Petersen and Kitchell 2001*; Marine and Cech 2004)
		↓ adult survival due to stress from temperature or disease	migration delays, higher stray rate		earlier adult migration ↑ disease resistance ↑ energetic efficiency at high temperatures	(McCullough 1999; Hyatt et al. 2003; Naughton et al. 2005; Goniea et al. 2006; Battin et al. 2007)
		↓ reproductive success (↓ egg viability from thermal stress, or smaller eggs due to ↑ energetic cost)			shift reproductive allocation	(McCullough 1999; Kinnison et al. 2001; Rand et al. 2006)
↓ summer and fall flows	high	↓ parr survival	change habitat		(Crozier and Zabel 2006*)	
shorter and milder winter	high	↑ development rates	earlier emergence	↑ energetic efficiency at higher temperatures	(Beacham and Murray 1989; Finstad et al. 2004)	
↑ spring temperatures	high	↑ development rates	earlier smolt migration		(Beckman et al. 1998; Achord et al. 2007*)	
		↓ smolt survival		↑ disease resistance earlier smolt migration ↑ heat tolerance	(Smith et al. 2003 * found no effect; Zabel et al. in press* negative effect)	
earlier spring freshet weaker spring freshet	high high	↓ smolt survival	earlier smolt migration		(Achord et al. 2007*) (Williams et al. 2005*; Achord et al. 2007*)	

delay in upwelling	low	↓ adult energetic cost (if not too hot) ↑ juvenile survival if arrival time does not change	larger eggs	↓ metabolic rates, change migration route	(Kinnison et al. 2001; Rand et al. 2006) (Logerwell et al. 2003; Scheuerell and Williams 2005*; Williams et al. 2005*; Zabel et al. 2006*; Waples et al. 2008*) (Welch et al. 1998; Walker et al. 2000; Portner and Knust 2007)
↑ ocean stratification, ↑ surface temperature acidification	high	↑ metabolic costs in surface water	↑ vertical migration shift locations delayed maturation		
	high	↓ growth rate			



## Legend

Figure 1. The freshwater range of Snake River spring/summer Chinook and Columbia River sockeye salmon. These Chinook salmon rear in the Salmon River Basin, and sockeye salmon rear in Osoyoos Lake and Lake Wenatchee. The major dams along the migration route are shown with an \*. Bonneville (Bonn.) and Lower Granite (L.G.) dams are mentioned in the text.

Figure 2. Life cycles for seven genera of Pacific salmonids, illustrating the variety and complexity of anadromous life cycles in salmon, from Xanthippe Augerot, 2005. *Atlas of Pacific Salmon: The First Map-Based Status Assessment of Salmon in the North Pacific*. Univ. California Press.

Figure 3. A. Average daily Chinook salmon counts and temperatures at Lower Granite Dam from 1995 to 2006. The boxed area shows the average time period the river is over 20°C, reducing the migration of adults, as shown by the lower Chinook counts during this time period. B. Mean July temperature at Bonneville Dam, with 1960-1979 temperatures inferred from measurements at McNary Dam. Median migration date of C. spring Chinook and D. sockeye salmon. Regression statistics and lines are shown. All data from DART 2007.

Figure 4. Hypothetical interaction between shifts in life cycle timing and shifts in environmental optima. The X-axis represents time from spawning through ocean entry. Dashed vertical lines show the current phenotype. The line shifts for emergence, downstream migration, and ocean entry timing represent plastic changes in phenology. The upper graph represents an equilibrium condition with the response of the fish adapted to environmental conditions. The second row shows a hypothetical climate-change scenario with optimal migration timing shifted earlier, spawn timing shifted later, emergence and downstream migration timing shifted earlier, and ocean entry shifted later. The third row shows the likely physiological (plastic) response to warmer temperatures in relation to the climate-shifted optima, and the potential mismatch between optimal and realized phenology. The bottom row shows the potential evolutionary response to the mismatches depicted in the third row. Note that earlier downstream migration but later ocean entry would seem to present contradictory pressures.

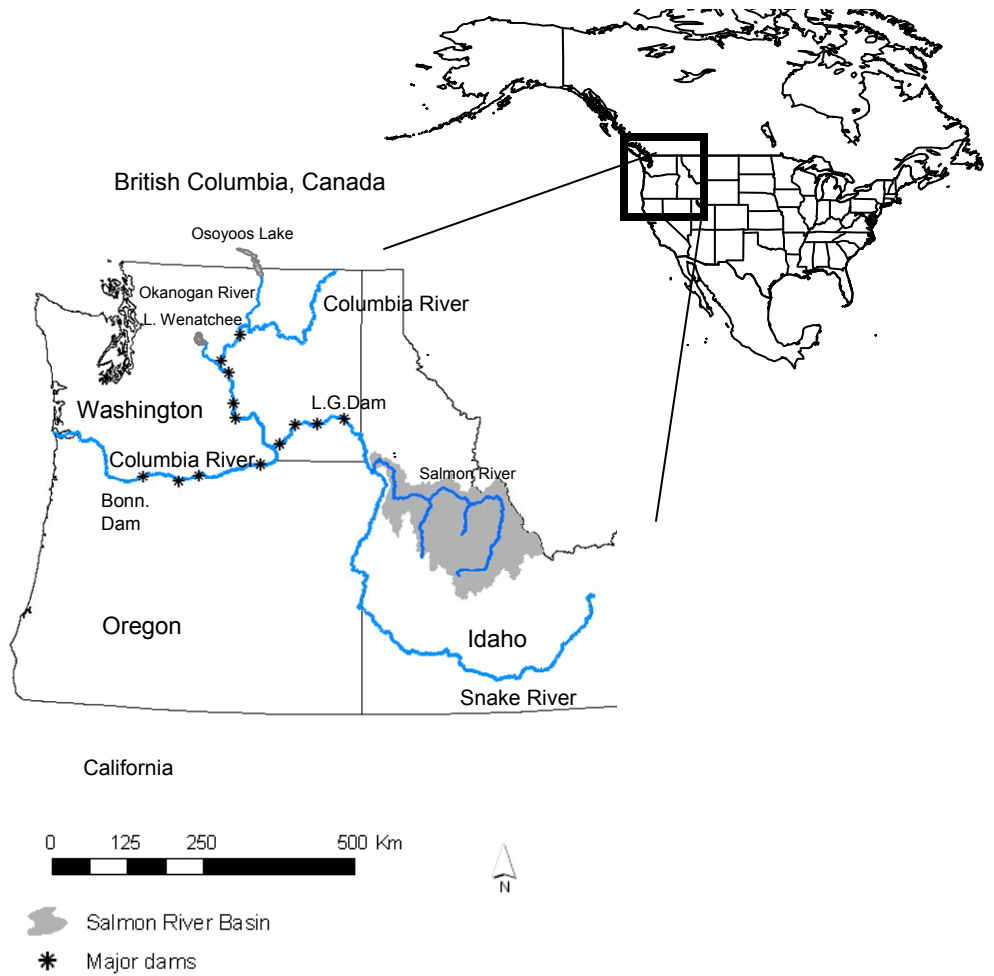


Fig. 1

# Salmon Life Cycle

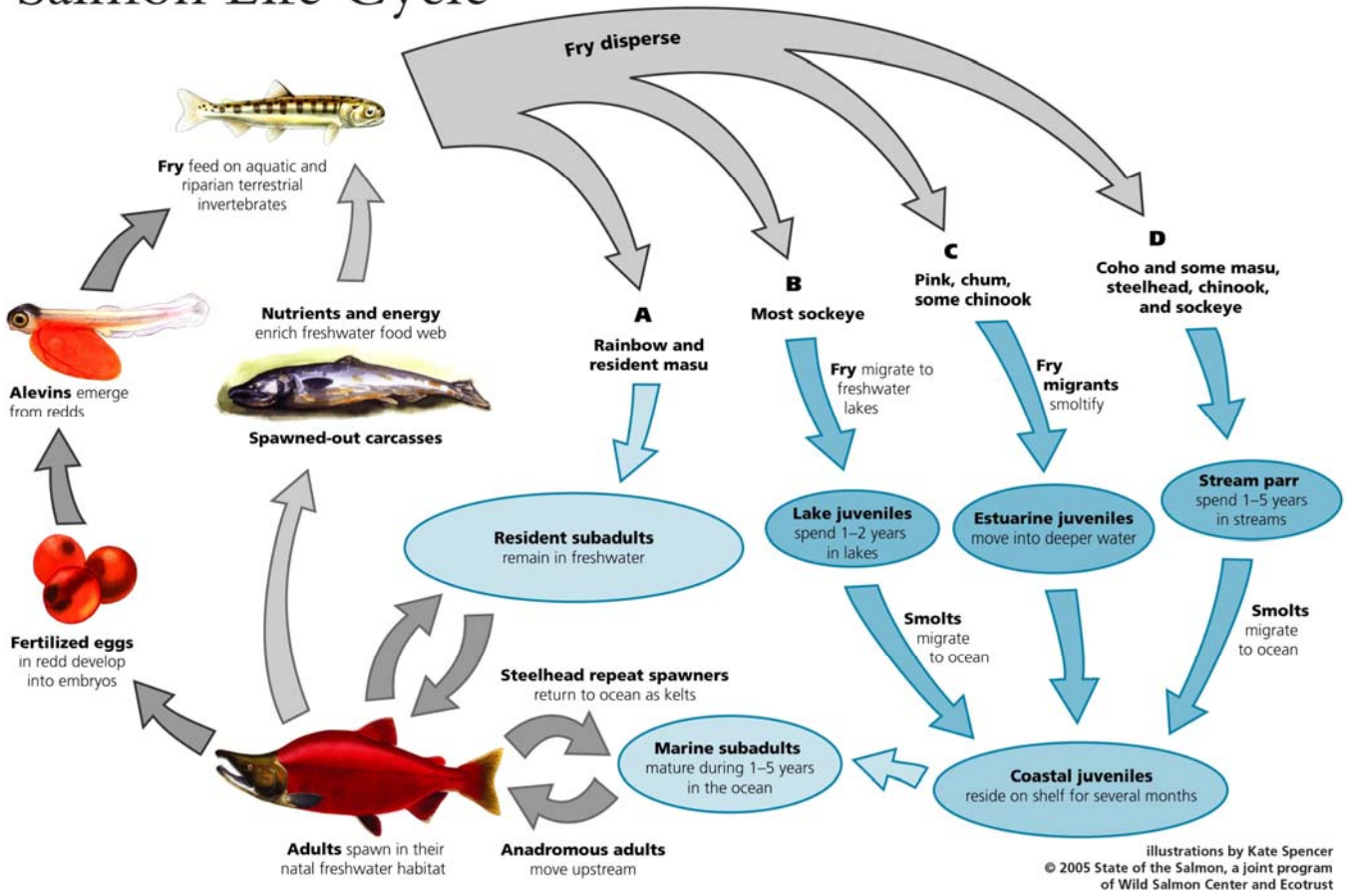


Fig. 2



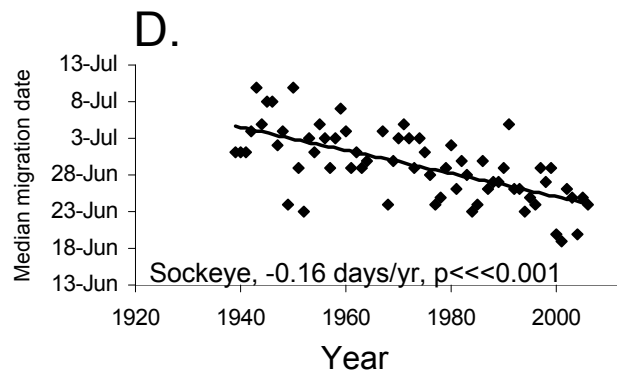
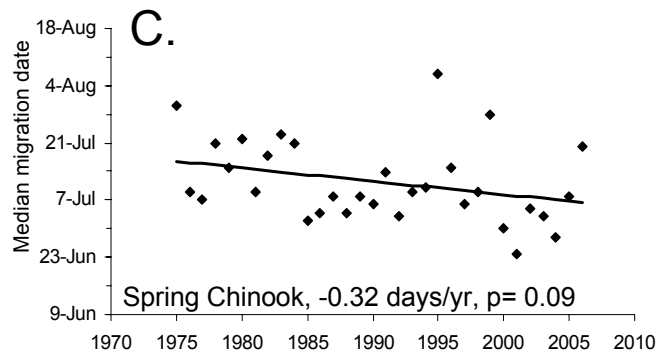
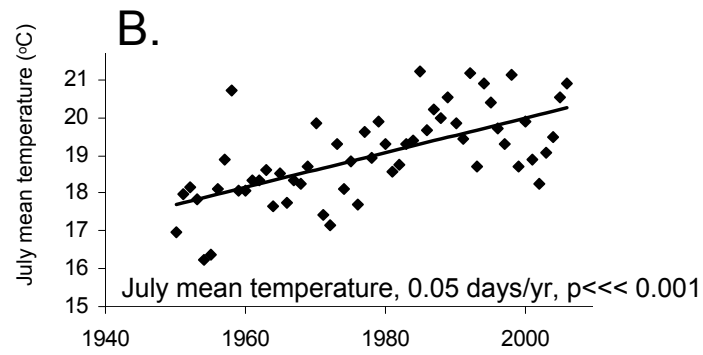
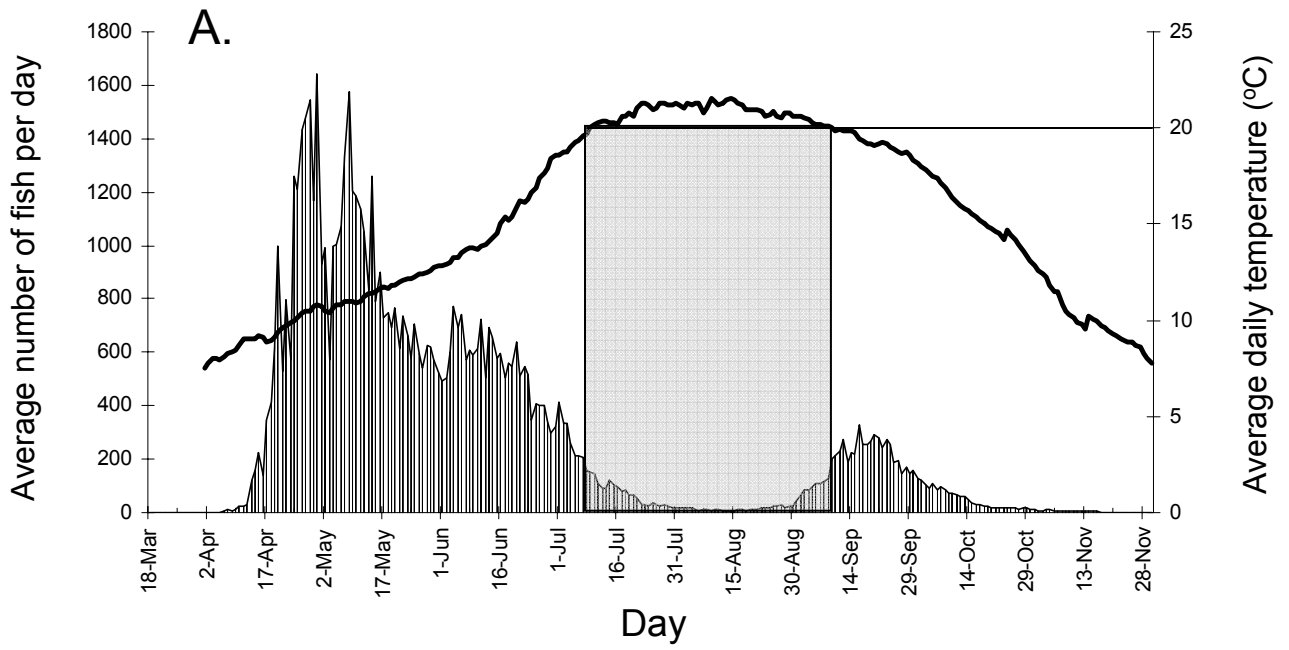


Fig. 3

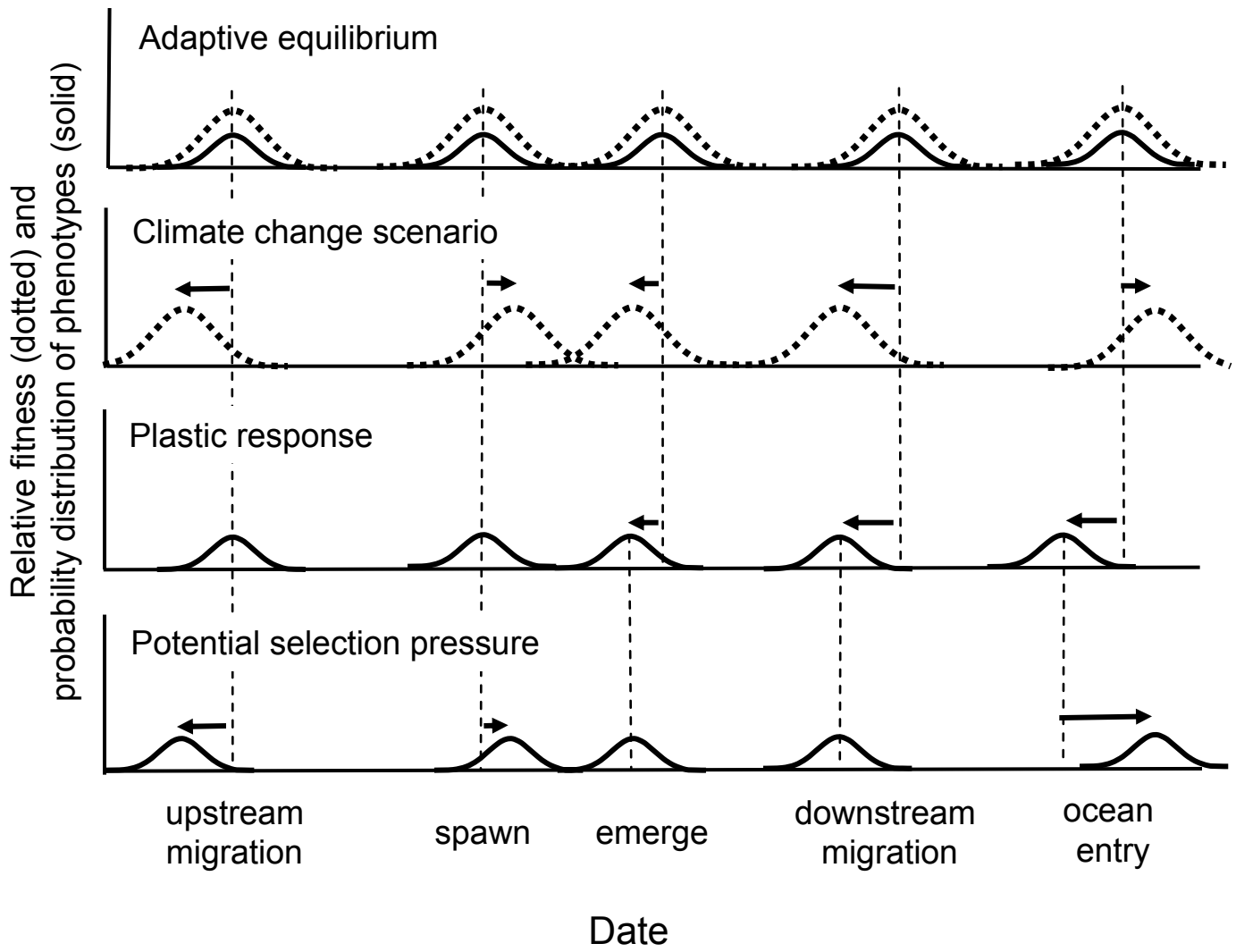


Fig. 4