

1 **Threatened salmon rely on a rare life history strategy in a warming**
2 **landscape**

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23 **Abstract**

24 Rare phenotypes and behaviors within a population are often overlooked, yet they may
25 serve a heightened role for species imperiled by rapid warming. In threatened spring-run
26 Chinook salmon spawning at the southern edge of the species range, we show late-migrating
27 juveniles are critical to cohort success in years characterized by droughts and ocean heatwaves.
28 Late migrants rely on cool over-summer river temperatures, increasingly rare due to the
29 combined effects of warming and impassable dams. Despite the dominance of late migrants,
30 other strategies played an important role in many years. Our results suggest that further loss of
31 phenotypic diversity will have critical impacts on population persistence in a warming climate.
32 Predicted thermally suitable river conditions for late migrants will shrink rapidly in the future,
33 and will be largely relegated above impassable dams. Reconnecting diverse habitat mosaics to
34 support phenotypic diversity will be integral to the long term persistence of this species.

35 **Main text**

36 Climate change is arguably the greatest emerging threat to global biodiversity and
37 ecosystem functioning in this period of unprecedented change^{1,2}. To track changing climate
38 regimes, many species have shifted their phenology³, distribution^{4,5}, and abundances⁶. While
39 there has been considerable attention given to predicting species and community-level
40 phenological responses to climate change^{7,8}, far less attention has been given to understanding
41 how the loss of within population variation and rare phenotypes might modulate population
42 resilience to future climate forcings^{9,10}.

43 Phenotypic diversity is one way for populations to buffer themselves against natural or
44 anthropogenic perturbations¹¹⁻¹³. Plasticity in migratory timing may be particularly important
45 for species that migrate between freshwater and marine environments to forage and spawn, as
46 their ability to respond to adverse ambient conditions is constrained by the stream network,
47 leaving fewer options for lateral movements compared with terrestrial or marine species¹⁴⁻¹⁷.
48 Furthermore, in many cases, anthropogenic land use changes, such as hydropower dams and

49 irrigation diversions, have restricted access to high elevation habitats that would have
50 otherwise provided thermal refugia^{18–20}.

51 Salmonids exhibit extensive phenotypic plasticity, which could enhance population
52 stability against disturbances by spreading risk across time and space (portfolio effect
53 concept^{12,21,22}). However, multiple concurrent environmental forcings could weaken this
54 portfolio effect and challenge species resilience to future climate change²³. In particular, the
55 combination of warming and habitat contraction, caused by dam construction, has resulted in
56 large population declines and erosion of salmon life history diversity, particularly for runs that
57 rely on cooler high elevation habitats^{24,18,25,26}. To understand how life history diversity may
58 influence salmon resilience to climate change, we tracked the relative contribution of different
59 juvenile migratory strategies in California’s Chinook salmon (*Oncorhynchus tshawytscha*)
60 populations that spawn in a heavily modified environment at the southern edge of the species’
61 native range²⁷. These salmon serve as a model system for early indication of the challenges
62 faced by cold-water fishes when access to thermal refugia has been drastically reduced²⁸.

63 While juvenile salmonids at higher latitudes often spend multiple years in freshwater
64 before emigrating to the ocean^{27,29}, today, most salmon in the California Central Valley
65 emigrate in their first winter and spring before river temperatures become too warm. An
66 exception is found among spring-run Chinook salmon that used to dominate the region before
67 the construction of impassable dams²⁴. Two populations still have access to high elevation
68 reaches, and exhibit a now rare phenotype where juveniles remain in the river over-summer
69 before emigrating the following fall³⁰. This late-migrating phenotype relies on access to cool
70 water for the entire rearing period and is therefore most likely to be negatively impacted by
71 warming temperatures and impaired access to high elevation reaches. Here, we used strontium
72 isotope ratios (⁸⁷Sr/⁸⁶Sr) and daily depositional chronology in otoliths (calcium carbonate
73 structures, part of the fish’s hearing and balance system) to reconstruct the juvenile emigration
74 patterns and growth rates of returning (i.e., successful) adult spring-run Chinook salmon, and to
75 estimate the contribution of different migration strategies to the reproductive population
76 across environmental extremes. Specifically, ⁸⁷Sr/⁸⁶Sr vary among California Central Valley

77 rivers, producing distinct and reproducible geographic markers across the landscape that are
78 permanently recorded in the daily otolith layers, thus allowing reconstruction of the juvenile
79 life histories of 123 adults that returned to Mill and Deer Creeks (two geographically close
80 watersheds with genetically similar spring-run populations³¹; Fig. 1a) between 2007 and 2018
81 (Supplementary Table 1). Some of these cohorts experienced severe droughts and warm ocean
82 conditions (Supplementary Table 2) revealing potential mechanisms involved in the expression
83 and success of alternative life history strategies. We also investigated how predicted future
84 river temperatures will affect the availability of suitable rearing habitat and the long-term
85 viability of the late-migrating phenotype. In summary, we show how climate change may
86 truncate salmon life history diversity, and how the loss of the late-migrant phenotype could
87 negatively affect the long-term resilience of threatened spring-run Chinook salmon populations.

88

89 **The importance of rare phenotypes and life history diversity**

90 Otolith isotope profiles revealed three distinct juvenile life-history types (hereafter
91 referred to as “early”, “intermediate” and “late” migrants; Fig. 1b-d, Supplementary Fig. 1),
92 concordant with the three emigration modes observed in the juvenile trapping data (Fig. 2a).
93 The three life-history types were characterized by significant differences in the age and size at
94 which the fish exited the natal tributary (Fig. 1b-d, 2b, Supplementary Fig. 2c, 2e). Despite
95 leaving the natal stream considerably smaller, early migrants entered the ocean at a similar size
96 and age to intermediate migrants, after rearing for multiple months in non-natal freshwater
97 habitats (i.e., Sacramento River and Delta). Late migrants emigrated to the ocean significantly
98 later and larger than the other two phenotypes (Fig. 2c, Supplementary Fig. 2d, 2f), having
99 reared in the natal stream over the summer (mean natal rearing period = 194 days \pm 32 days
100 SD). Late migrants may thus experience very different freshwater, estuarine and nearshore
101 marine conditions, potentially resulting in differential feeding, growth and survival
102 opportunities^{32,33}.

103 While late migrants were the rarest phenotype (10%) observed in juvenile monitoring
104 traps³⁴, they represented the majority (60%) of the returning adults averaged across years (Fig.
105 2a, 2b). Conversely, on average, 26% of juveniles and 19% of surviving adults were represented

106 by intermediate migrants that reared in natal rivers for 84 days \pm 27 days SD. Early migrants,
107 that reared in natal rivers for 15 days \pm 14 days SD, were the dominant phenotype observed in
108 juvenile monitoring (64%), yet their contribution to the adult returns was suppressed (only
109 21%). Importantly, the contribution rate of each life history type varied considerably among
110 years (Fig. 3). Half of the return years (2007, 2008, 2013) were represented by similar
111 contributions of each life history type, and their most likely emigration years (2004 & 2005,
112 2005 & 2006, 2009 & 2010) were generally wetter. In contrast, the late migrants that left
113 freshwater in the fall during multi-year droughts and ocean heatwaves (returning 2012, 2014,
114 2018) were functionally the only strategy to survive to adulthood (100%, 77%, and 97% of late
115 migrants observed respectively, Fig. 3; Supplementary Table 2).

116 Although variability in juvenile growth rates was observed, likely related to a
117 combination of fine-scale habitat heterogeneity and individual ontogeny, some clear trends
118 emerged from the otolith increment analysis. First, early-life freshwater growth rates were
119 inversely correlated with emigration timing, with faster growing individuals tending to leave the
120 natal tributary earlier, and slower growing individuals remaining for longer before migrating
121 downstream (Fig. 4a and Supplementary Fig. 3). Second, cumulative growth over the first 15
122 days was significantly faster for early migrants (37 $\mu\text{m} \pm 11 \mu\text{m}$ SD) compared to late migrants
123 (30 $\mu\text{m} \pm 8 \mu\text{m}$ SD) but not different between early and intermediate migrants (32 $\mu\text{m} \pm 7 \mu\text{m}$
124 SD; Fig. 4b). It is interesting to note that the fastest growth rates were typically observed
125 among the juveniles that left the natal stream earliest (within 15 days after emergence; open
126 circle dots in Fig. 4a), and thus also reared in non-natal habitats. Those results are consistent
127 with previous studies showing differential salmon juvenile growth rates and sizes across
128 multiple migratory pathways^{29,35}.

129 **Thermally suitable habitat in a warming climate**

130 Temperature strongly influences salmonid physiology, growth and survival³⁶. Thus,
131 populations with access to diverse water temperatures during incubation and natal rearing are
132 predicted to exhibit increased phenotypic and phenological diversity³⁷. To support late
133 migrants, stream temperatures need to remain suitably cool (temperature below $\sim 15^{\circ}\text{C}$ ³⁸) over

134 the summer to accommodate the extended rearing period. Mill and Deer Creek watersheds,
135 along with upstream reaches of the Battle and Clear Creeks, are among the few accessible and
136 populated spring-run streams in the system that still provide suitable rearing temperatures to
137 support all three phenotypes (Fig. 5 top panels). In accessible stream reaches where spring-run
138 Chinook were historically present but are now extirpated, only the Stanislaus River has
139 temperatures that could support the late migrating phenotype. Adult spring-run Chinook
140 (based on return timing) have recently been observed in the Stanislaus River suggesting this
141 habitat has the potential to support recolonization thus contributing to the reintroduction
142 efforts in the San Joaquin Basin³⁹. Importantly, increases in spring and summer stream
143 temperatures by 2040 (Extended Data Fig. 1) and 2080 (Fig.5 bottom panels) are predicted to
144 further contract the amount of thermally suitable rearing habitat, especially along the
145 downstream reaches of spring-run streams and the mainstem Sacramento River. Without
146 intervention, late-migrants may only have access to 76 km of suitable summer rearing habitat
147 by 2080, less than half (44%) of the accessible suitable habitat during our study period (i.e.,
148 2005-2015; Supplementary Table 3). Providing access above dams on the Sacramento, Feather,
149 Yuba, American, and Tuolumne Rivers (Fig. 5) would approximately triple summer rearing
150 habitat under 2080 climate conditions (76km without access, 201km with access;
151 Supplementary Table 3).

152 **Discussion**

153 Here, using archived otolith tissues, we reveal how a diversity of growth rates and
154 behaviors expressed during early life stages can shape population dynamics and resilience via
155 within-population portfolio effects. This underscores why it is essential that conservation
156 strategies developed for the recovery of vulnerable species support both rare and common
157 phenotypes. The phenotypic diversity expressed by California Central Valley spring-run Chinook
158 salmon has thus far enabled these populations to persist despite habitat loss and degradation
159 along their migratory corridor, warming temperatures, and an increasingly volatile
160 Mediterranean climate^{24,40}. We show for the first time that the late-migrating strategy is the
161 life-support for these populations during current periods of extreme warming. Therefore,

162 conservation priorities should focus on supporting this rare and climate-adapted behavior,
163 particularly given that climatic extremes such as extended droughts and marine heatwaves are
164 predicted to increase in frequency and severity in the future^{41,42}. Late migrants experience very
165 different selective pressures to the other migratory phenotypes, during both their freshwater
166 and ocean phases. For example, entering the ocean in a different season at a larger size
167 potentially reduces intraspecific competition and risk of mismatch with peak prey production
168 during early ocean residence, a critical period for cohort success⁴³. However, by rearing over
169 summer in freshwater late migrants forgo growth opportunities that early and intermediate
170 migrants experience by feeding earlier in the more productive ocean. This within-population
171 phenotypic diversity is thus critical to spreading risk and ensuring that at least some fraction of
172 the population is successful under differing environmental conditions.

173 For salmon and other species impacted by habitat contraction, restoring and maintaining a
174 diverse mosaic of habitats and thermal refugia across the freshwater landscape will be critical
175 to support life history diversity and long term persistence²². For spring-run Chinook salmon,
176 predicted stream temperatures under our climate change scenarios demonstrate the necessity
177 for maintaining and expanding thermally suitable rearing habitat in order to support diverse
178 growth rates and a broad spread of emigration timings. Juvenile salmon in the Central Valley
179 are known to experience high mortality rates during their seaward migration in the spring
180 particularly during droughts^{44,45}. This is further evidenced by the poor representation of early
181 and intermediate migrants in the adult returns in 2012, 2014 and 2018, which were all
182 characterized by hot and dry emigration conditions. Late migrants have evolved a drought-
183 resilient strategy of leaving in the fall when the migratory corridor is cooler, but they must be
184 able to survive the heat of the spring and summer in headwater habitats for this to be a viable
185 strategy. Improving access to cold water refugia through habitat restoration, targeted water
186 management below dams, and/or reintroductions to high elevation habitats above impassable
187 dams, might be vital for preserving the late migrant life-history type now and under future
188 climate scenarios^{46,47}. While the predicted amount of summer rearing habitat above dams may
189 be modest under 2080 conditions (125km; Supplementary Table S3), this reliable cold water
190 could play a disproportionate role in preventing extirpation during multi-year droughts. In

191 addition, improving growth and survival conditions for early and intermediate migrants along
192 degraded migratory corridors could be instrumental to bolster productivity and resilience,
193 particularly in wetter years when earlier migrants play an important role in population success.

194 Salmonid species are renowned for their extensive migratory plasticity, with
195 anadromous forms spending a few months to many years in freshwater⁴⁸. While phenotypic
196 trait diversity in salmon species is often discussed in the context of genetic differentiation and
197 microevolution^{49,50}, the life history diversity observed in these genetically similar spring-run
198 populations³¹ highlights the important interaction between physiology and environmental
199 variability in the expression of divergent juvenile emigration strategies⁵¹. Although physiological
200 plasticity can increase species' resilience to climate change⁵², it is unclear whether salmonids
201 can adapt their thermal tolerances quickly enough to keep pace with predicted rates of
202 warming. This is particularly problematic for populations at lower latitudes⁵³ and those facing
203 additional stressors (e.g., contaminant loads, limited food) that further contract their thermal
204 window by affecting their metabolic performance⁵⁴. As environmental conditions continue to
205 shift rapidly with climate change, maximizing habitat options across the landscape to enhance
206 adaptive capacity and support climate-resilient behaviors may be crucial to prevent extinction
207 events within salmonids and other thermally vulnerable species^{23,52,55}.

208

209 **Methods**

210 **1. Otolith ⁸⁷Sr/⁸⁶Sr analysis**

211 Otoliths were prepared at UC Davis per established techniques⁵⁶. The otoliths' sagittal
212 plane (see Fig 3. in Woodson et al.³²) was sectioned on both sides using 600 and 1500 grit
213 wet/dry sandpaper to expose the primordia and surrounding microstructure. The surface
214 achieved a further fine polish using 3µm and 1 µm Al₂O₃ lapping films. Finished samples were
215 mounted to a 1cm square glass pedestal using Gorilla Glue™. The otoliths' dorsal side was
216 photographed in 20x magnification using a Qimaging digital camera (MicroPublisher 5.0 RTV)
217 mounted to a Olympus BX60 microscope. Following imaging otoliths were analyzed for

218 strontium isotopes at the UC Davis Interdisciplinary Center for Inductively-Coupled Plasma
219 Mass Spectrometry by laser ablation on their Multi Collector Inductively Coupled Mass
220 Spectrometer. We used the otolith strontium isotope methods described in Barnett-Johnson et
221 al.^{57,58} to reconstruct juvenile freshwater habitat-use and migration histories. In brief, the
222 strontium isotope ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) of freshwater habitats (the “isoscape”) varies as a function of
223 rock geology and weathering patterns⁵⁹, and because there is no biological fractionation of
224 strontium isotopes, the otoliths faithfully record the signature of the surrounding water and
225 dietary sources. Strontium isotopes are a particularly powerful tool in the California Central
226 Valley, because the spatial heterogeneity in rock types results in significant differences in
227 isotope signatures among most of the salmon-bearing watersheds. Consequently, variations in
228 $^{87}\text{Sr}/^{86}\text{Sr}$ and strontium concentration across Central Valley watersheds has proven useful for
229 determining population of origin^{58,60} and reconstructing juvenile rearing and migration
230 behavior^{44,61}.

231

232 **2. Movement reconstruction**

233 Otolith radius was used as a proxy for fish size at natal and freshwater exit (see
234 Supplementary Information section 2.2). The otolith radius for each $^{87}\text{Sr}/^{86}\text{Sr}$ measurement was
235 estimated by measuring the distance from the otolith core to the center of each laser pit along a
236 standardized 90° axis⁵⁶. Strontium isotope profiles representing changes in $^{87}\text{Sr}/^{86}\text{Sr}$ values as a
237 function of otolith distance from the core were created for each otolith. Specific location $^{87}\text{Sr}/^{86}\text{Sr}$
238 threshold values were used to identify the movement of Central Valley spring-run Chinook
239 juveniles from one rearing region to the other. These values come from a Central Valley isoscape
240 database⁶¹. We considered four distinct regions in this study: Natal tributary (i.e., Mill and Deer
241 Creeks), Sacramento River, Sacramento-San Joaquin Delta (hereafter “Delta”), and San Francisco-
242 San Pablo Bay (hereafter “Bay”) & Ocean. We used changes in $^{87}\text{Sr}/^{86}\text{Sr}$ along the otolith transect
243 to identify two key habitat shifts to reconstruct the size at which individuals exited (1) the natal
244 tributary, and (2) freshwater (exit location is Chipps Island, river kilometer 73). Otolith radius at
245 natal exit was calculated by linearly interpolating between otolith distances at the $^{87}\text{Sr}/^{86}\text{Sr}$

246 measurements on either side of the upper Sacramento River (point of Mill and Deer Creek exit
247 and Sacramento River entry) strontium threshold value. We used the lowest $^{87}\text{Sr}/^{86}\text{Sr}$ value found
248 for the upper Sacramento River region in the Central Valley isoscape database. If for a given fish
249 this threshold was never crossed (i.e., $^{87}\text{Sr}/^{86}\text{Sr}$ values are all above the threshold), we
250 determined it by visually identifying the closest point to the Mill/Deer Creek habitat $^{87}\text{Sr}/^{86}\text{Sr}$
251 threshold value in the strontium profiles. This could happen if a fish migrated quickly after
252 emergence to the Sacramento River, which is characterized by higher $^{87}\text{Sr}/^{86}\text{Sr}$ values than the
253 natal tributary. Similarly, otolith radius for freshwater exit was calculated by linearly interpolating
254 between otolith distances at the $^{87}\text{Sr}/^{86}\text{Sr}$ measurements on either side of the Chipps Island (point
255 of Delta exit and Bay entry) strontium threshold value. Finally, the Sacramento River at Freeport
256 $^{87}\text{Sr}/^{86}\text{Sr}$ value threshold was used to identify the migration of spring-run juveniles from the
257 mainstem Sacramento River to the Delta.

258

259 **3. Clustering analysis**

260 We conducted a clustering analysis⁶² on the strontium profiles obtained from the otolith
261 microchemistry analysis to investigate whether we could statistically identify groups of fish
262 exhibiting similar juvenile rearing strategies among Mill and Deer Creek populations. Strontium
263 profiles were considered as smooth curves or functions sampled at a finite subset of some
264 interval (here the distance from the otolith core); the statistical methods for analyzing such
265 data are described as “Functional Data Analysis” (FDA; see Ramsay and Silverman⁶³ for an
266 overview of FDA). With FDA methods each profile is modeled in an infinite functional space
267 rather than considered as a discrete vector in a multidimensional space (as modeled in
268 multivariate data analysis). The clustering analysis performed in this paper included the
269 following steps:

- 270 1) A smoothing spline was fitted to each profile to predict continuous $^{87}\text{Sr}/^{86}\text{Sr}$ values
271 for otolith radius distances between 0 and 1000 μm (using the *smooth.spline*
272 function in R⁶⁴). This allows us to obtain a smooth version of the profiles for any

273 distance from the otolith core to 1000 μm so that a direct comparison of all Mill and
274 Deer Creek strontium profiles of different lengths can be achieved.

- 275 2) Each smoothed profile was then transformed into a functional data object (i.e.,
276 decomposed in terms of linear combinations of known basis functions), using a B-
277 splines basis (using the *fda* package in R⁶³).
- 278 3) A functional principal component analysis (FPCA) was performed on those functional
279 objects (using *fda* package in R). This allowed us to identify the principal modes of
280 variation of the functional dataset, and reduce data dimensions which has been
281 shown to help for clustering pattern recognition and processing time⁶².
- 282 4) We used a model-based clustering method, where the data were represented by a
283 series of Gaussian Mixture Models (GMM) for which each point (i.e., each profile)
284 was associated with a probability of belonging to each potential cluster⁶⁵. The
285 mixture model parameters were estimated using the Expectation-Maximization (EM)
286 algorithm.
- 287 5) The Bayesian Information Criterion (BIC) was used to select the best model with the
288 optimal number of clusters (using *mclust* package in R⁶⁶).

289

290 **4. Early-life growth rate estimation**

291 To estimate habitat-specific juvenile growth rates we measured the otolith increment
292 widths using Image Pro Premier 9.0 (Media Cybernetics) in each isotopically distinct habitat
293 region⁵⁶. Each otolith reading was assigned a score of “certainty” on a scale of 1-5, with 1 =
294 unusable, 2 = hard to read the majority of increments, 3 = hard to read some of the increments,
295 4 = easy read, and 5 = perfect publication quality. This index is a combination of the reader’s
296 confidence in the accuracy of the increment placement and the quality or readability of the image
297 (i.e., how likely it is that another reader would get the exact same increment width
298 measurements). Otoliths with poor readability (with a score of 3 or lower) were eliminated from
299 the analysis. A total of 86 otoliths were used for growth rate estimations.

300 **5. Central Valley spring-run streams temperature suitability mapping**

301 To explore why Deer and Mill Creeks may exhibit multiple juvenile life histories and how life
302 history expression may change with climate change, we compared current and future thermal
303 conditions along every current and historical spring-run stream. Temperature was obtained
304 from a mean monthly stream temperature model²⁰. In brief, FitzGerald et al.²⁰ employed a
305 spatial stream temperature model to predict mean monthly stream temperature for nearly
306 every river km in the western U.S. In the Central Valley, the test sample r^2 was 0.813 and the
307 mean absolute prediction error (MAPE) was 1.024°C. We first clipped this stream temperature
308 dataset with the current and historical Central Valley spring-run distributions⁶⁷. In general, the
309 distribution and stream networks matched, but a few reaches with spring-run did not have
310 stream temperature. We averaged the monthly temperature at each stream segment from
311 2005-2015, representing our study period. In the Central Valley, stream temperatures are
312 predicted to increase by 0.6°C by 2040 and 1.0°C by 2080⁶⁸, so we applied these deltas to the
313 temperature dataset.

314 We then examined stream temperature suitability for juveniles rearing in May and August
315 of 2005-2015, 2040, and 2080. We focused on months when temperature stress is most likely
316 to impact rearing success for early and intermediate migrants (May) and late migrants (August).
317 A river reach was defined as suitable when it provided optimal temperature for spring run
318 juvenile growth. Here we used a fixed temperature threshold of 15°C because temperatures
319 greater than ~15°C result in decreased growth rates and increased mortality rates, yet we
320 acknowledge that there is likely some variation in this threshold according to local water
321 quality, food availability, and the life stage considered^{54,69}.

322

323 **Data Availability**

324 The datasets generated and used for the otolith strontium isotope and early-life freshwater
325 growth analyses, and to produce Figs 1-4 & S1-S3 are available on GitHub at
326 <https://github.com/floracordoleani/MillDeerOtolithPaper>⁷⁰. The stream temperature and
327 spring-run Chinook spatial distribution shapefiles generated for the juvenile spring-run Chinook
328 thermal habitat suitability assessment and used in Figs 5 & S4 are available on DRYAD at
329 <https://doi.org/10.5061/dryad.bk3j9kdc9>⁷¹.

330

331 **Code Availability**

332 The code for the otolith strontium isotope and early life growth analyses is posted on GitHub at
333 <https://github.com/floracordoleani/MillDeerOtolithPaper>.

334

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355 **Author Contributions**

356 FC, CCP, PKW, AMS and RCJ conceived the study. FC led data collection and analyses. FC, CP, AMS,
357 AMF, PKW, AM, and RCJ contributed to data analyses and manuscript writing. GEW, CCP, and

358 PKW conducted the otolith microchemistry and microstructure analyses. AMF performed the
359 temperature prediction modelling and AM performed the clustering analysis.

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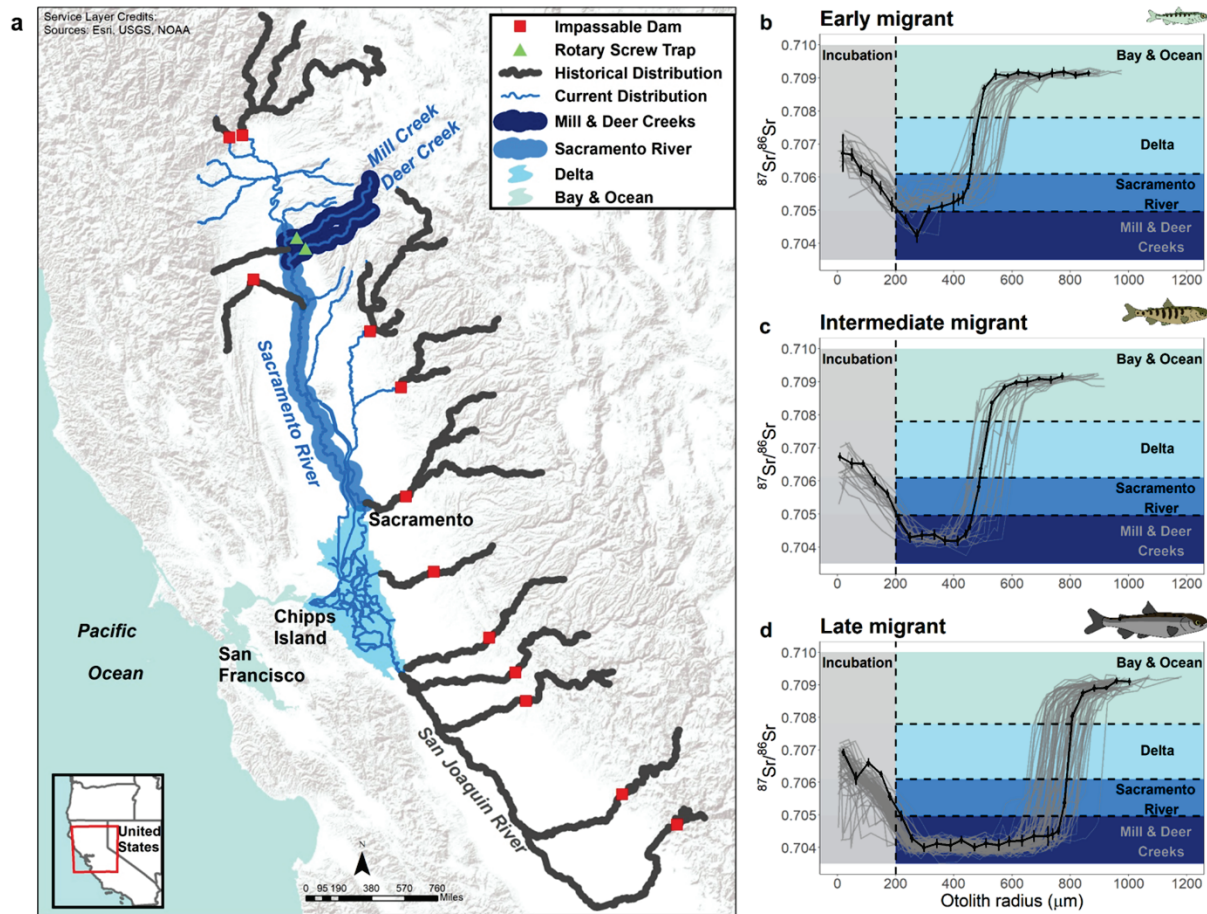
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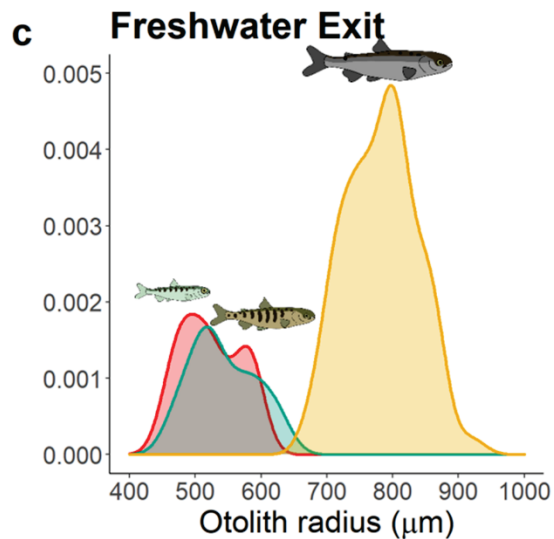
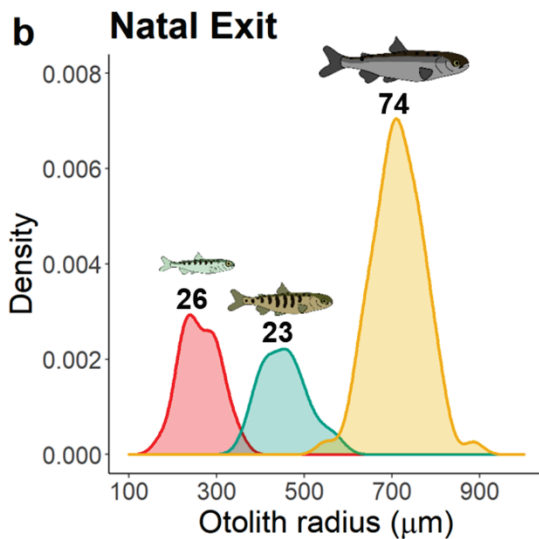
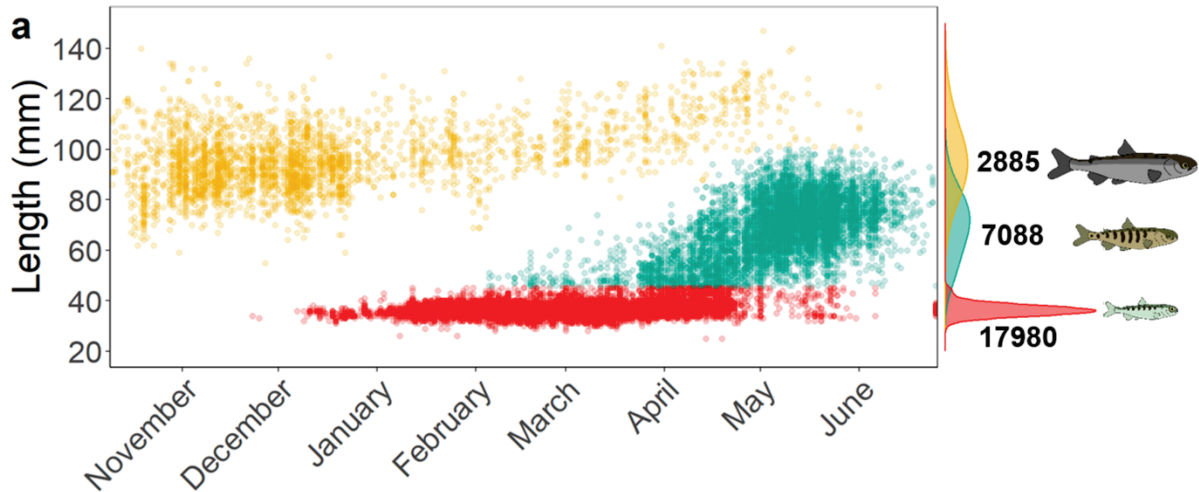
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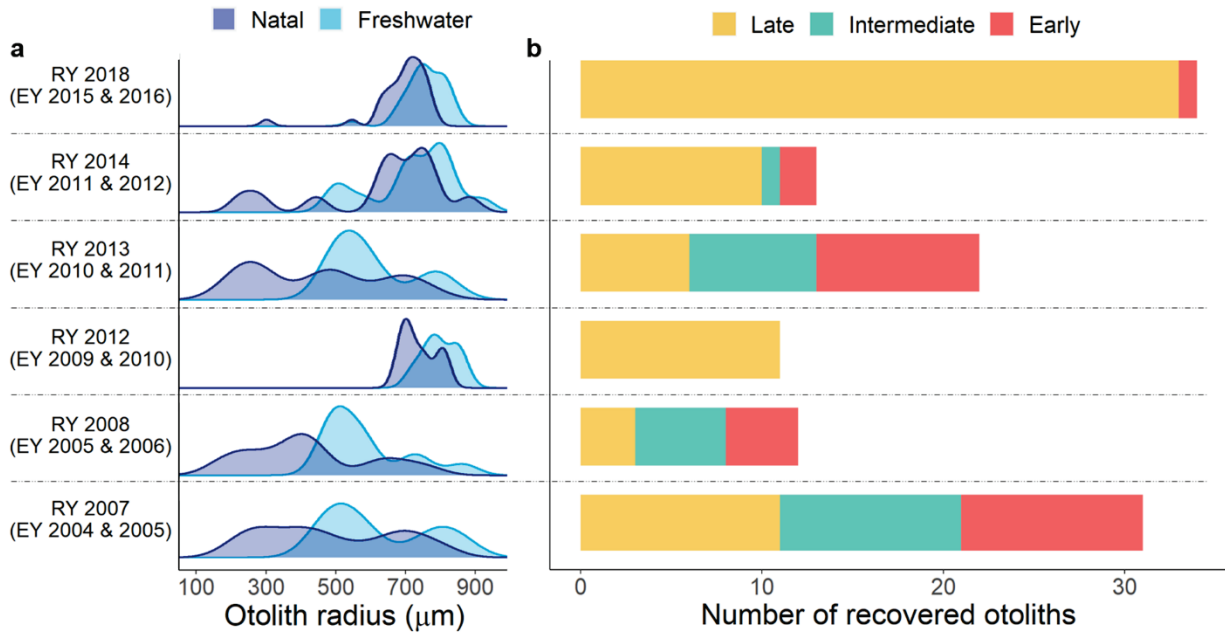
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 383 **Figure 1. Spring-run Chinook salmon life history diversity.** Left panel: map of historical and current
 384 distribution of California Central Valley spring-run Chinook salmon, with the two Lassen tributary
 385 populations in this study highlighted in dark blue. Delta = Sacramento-San Joaquin River Delta, Bay =
 386 estuary between Suisun and San Francisco Bays, and Chipps Island = freshwater exit location. Right
 387 panel: Otolith strontium isotope profiles (grey lines) separated into early, intermediate and late
 388 migrants. Life-history types were classified using cluster analyses based on otolith isotope-by-radius data
 389 for all years combined (see Methods and Supplementary Information section 1.2). A representative
 390 profile from each cluster ($\pm 2SD$) is shown in bold. The first part of the profile (0 to $\sim 200\mu\text{m}$; represented
 391 by a grey rectangle) corresponds to the incubation period when the fry is nourished by the maternal yolk
 392 in the gravel.

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395
 396 **Figure 2. Migrant size distributions at natal and freshwater exit.** (a) Raw catch data and size
 397 distribution of juveniles caught in the Mill and Deer Creek rotary screw traps between 1995 and 2010.
 398 Each color represents a life history type based on its size and date at emigration: red = early, green =
 399 intermediate, yellow = late migrants (see Supplementary Information section 2.1). Numbers near each
 400 density profile represent fish counts per life history type. Otolith radius (proxy for fish size) distributions
 401 for each life-history type when they emigrated out of the natal stream (b) and out of freshwater (c).
 402 Colors correspond to life history types denoted in Figure 1. Numbers above each density peak represent
 403 fish counts per life history type. Note that the juvenile emigration years associated with return years
 404 from the otolith analysis (2004-2015; Supplementary Table 2) do not entirely match with the emigration
 405 years from juvenile trapping data (monitoring performed from 1995 to 2010).

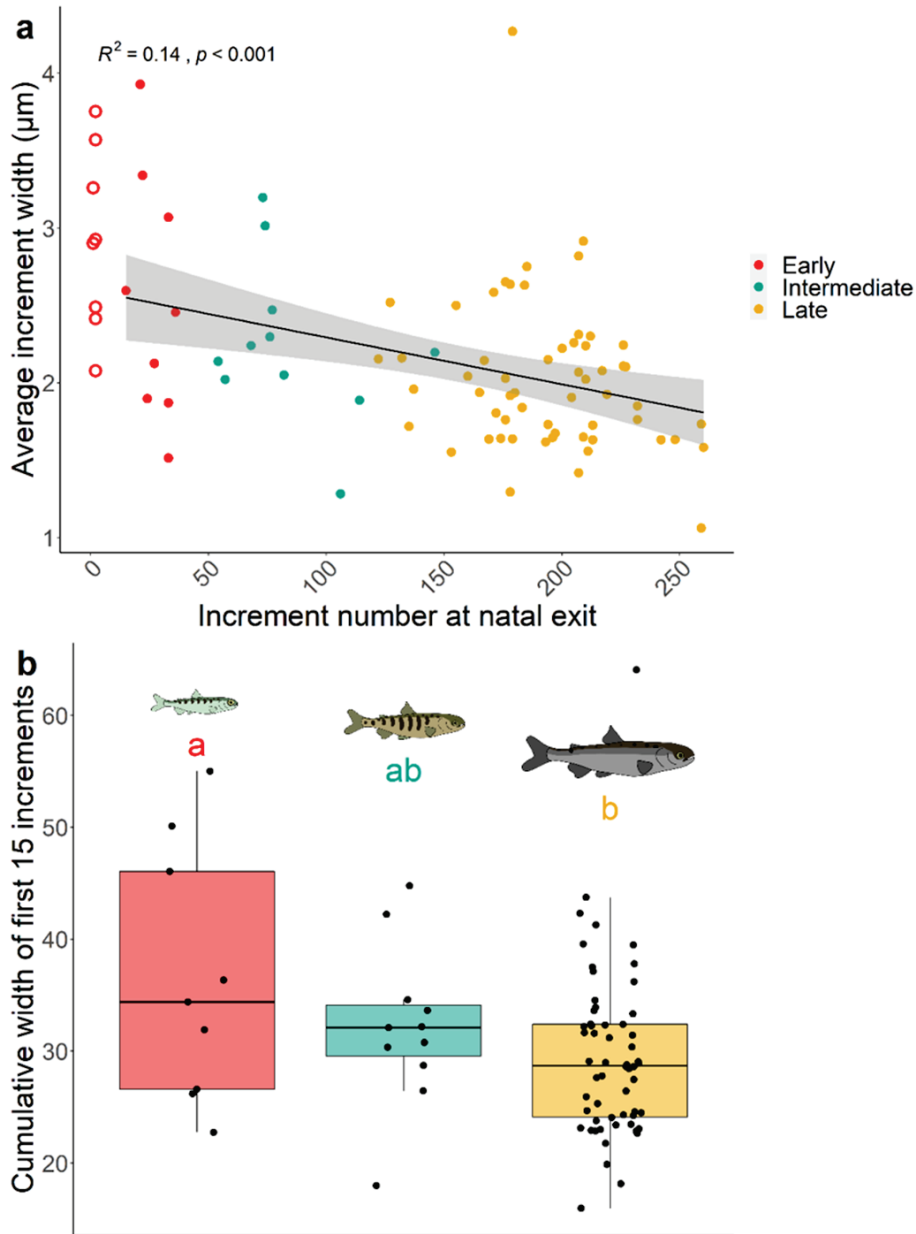
406



407

408 **Figure 3. Migrant sizes and life history diversity across years.** (a) Otolith radius (proxy for juvenile fish
409 size) distributions for each adult return year (RY) and its most likely juvenile emigration years (EY, shown
410 in parenthesis) at natal and freshwater exit, showing interannual differences in the size distribution of
411 the juvenile emigrants that survived to adulthood. Density distributions are standardized by year. (b)
412 Contributions of each life-history type to the adults returns. In multiple years, late emigrating juveniles
413 comprised the majority of returning adults.

414

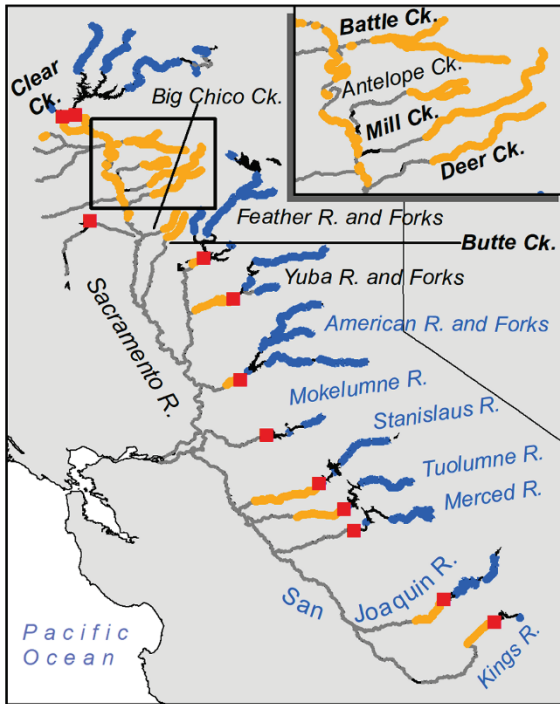


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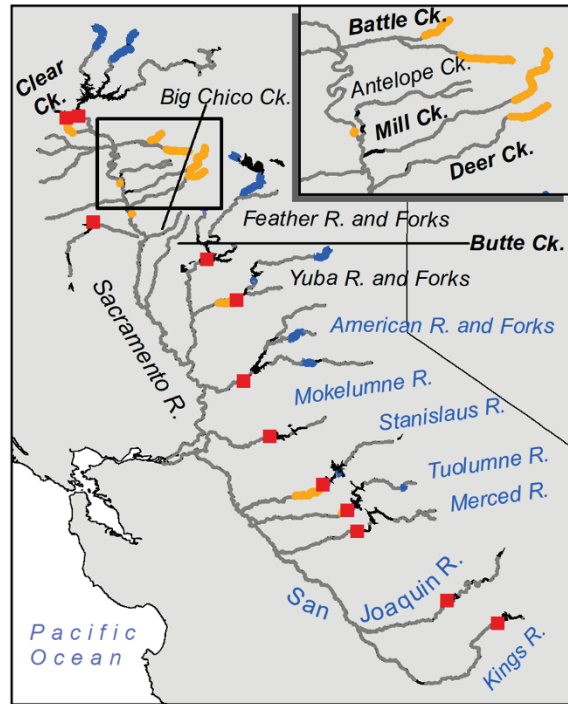
416 **Figure 4. Early-life salmon growth across life history types.** (a) Fish daily otolith increment width (a
 417 proxy for fish growth rate) averaged over the first 15 days after emergence and plotted against the
 418 otolith increment number (a proxy for age in days) at natal exit, for each life history type. Filled circles
 419 show individuals that were still in their natal tributary at day 15, and used for the early-life growth
 420 analysis, while open circles represent individuals that had left their natal tributary before day 15 and
 421 reared elsewhere. A linear regression is represented by the black line, with the grey shade showing the
 422 95% confidence interval. Even excluding the fast-growing individuals (open circles), there is a negative

423 relationship (R^2 and p -value) between age at natal exit and initial growth rates. (b) Boxplot comparing
424 cumulative increment width at day 15 (a proxy for somatic growth achieved in the first 15 days),
425 between the three migratory phenotypes. Only fish that spent at least 15 days in the natal stream were
426 included. The horizontal line in each box represents the median value, lower and upper hinges of the
427 boxes correspond to the 25th and 75th percentiles. The upper whiskers extend from the hinge to the
428 largest value no further than $1.5 \times \text{IQR}$ from the hinge. The lower whisker extends
429 from the hinge to the smallest value, $1.5 \times \text{IQR}$ of the hinge, at most. The black dots are the actual
430 measurements. Boxes not sharing the same letter are significantly different (Tukey test with significance
431 level $\alpha = 0.05$, $DF = 75$).

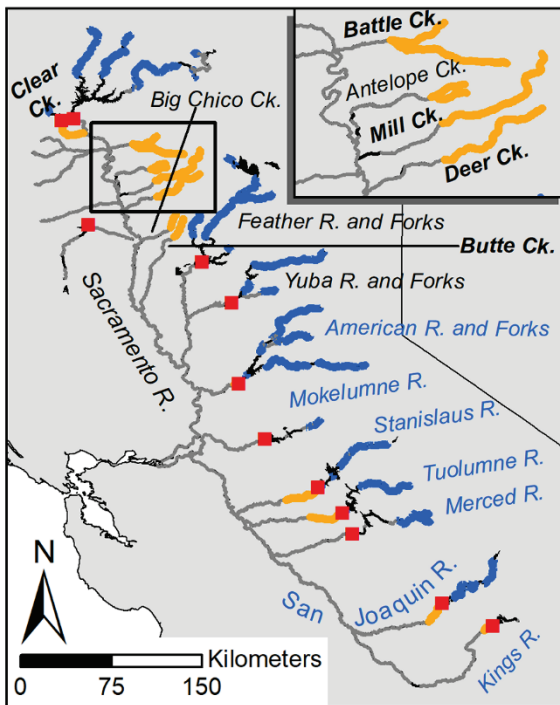
May - 2005-2015



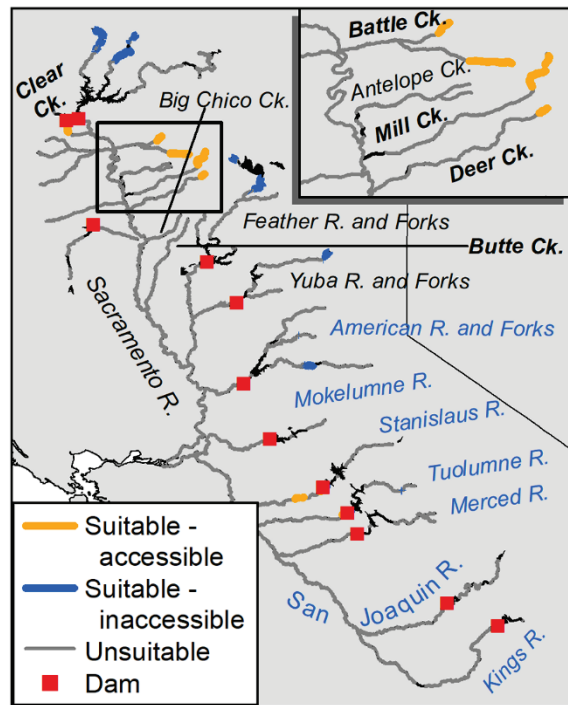
Aug - 2005-2015



May - 2080



Aug - 2080



432

433 **Figure 5. Central Valley habitat suitability mapping under current and future climate conditions.**

434 Rearing temperature suitability (temperature < 15°C³⁸) in accessible (orange lines) and inaccessible (i.e.,

435 blocked by impassable dam; blue lines) river reaches in the California Central Valley, focusing on months
436 when temperature stress is most likely to impact rearing success for early and intermediate migrants
437 (May; left panels) and late migrants (August; right panels). We examined suitability (defined as
438 temperature < 15°C, see Methods) during our study period (top panels) and under a future climate
439 change scenario (2080, bottom panels). The inset maps highlight our study streams (Mill and Deer
440 Creeks) and nearby spring-run streams. Major current and historical spring-run streams are labeled, with
441 extirpated populations in blue font, and populations at low risk of extirpation⁷² in bold. The gray lines
442 represent reaches that are thermally unsuitable for rearing (mean monthly temperature > 15°C). The
443 black lines represent reaches where temperatures could not be predicted reliably (e.g., reservoirs). See
444 Methods for details on temperature mapping.

445

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