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ARTICLES

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# Threatened salmon rely on a rare life history strategy in a warming landscape

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

Climate change is arguably the greatest emerging threat to global biodiversity and ecosystem functioning in this period of unprecedented change[1,2]. To track changing climate regimes, many species have shifted their phenology[3], distribution[4,5] and abundances[6]. While there has been considerable attention given to predicting species and community-level phenological responses to climate change[7,8], far less attention has been given to understanding how the loss of within-population variation and rare phenotypes might modulate population resilience to future climate forcings[9,10].

Phenotypic diversity is one way for populations to buffer themselves against natural or anthropogenic perturbations[11–13]. Plasticity in migratory timing may be particularly important for species that migrate between freshwater and marine environments to forage and spawn, as their ability to respond to adverse ambient conditions is constrained by the stream network, leaving fewer options for lateral movements compared with terrestrial or marine species[14–17]. Furthermore, in many cases, anthropogenic land use changes, such as hydropower dams and irrigation diversions, have restricted access to high-elevation habitats that would have otherwise provided thermal refugia[18–20].

Salmonids exhibit extensive phenotypic plasticity, which could enhance population stability against disturbances by spreading risk across time and space (portfolio effect concept[12,21,22]). However, multiple concurrent environmental forcings could weaken this portfolio effect and challenge species resilience to future climate change[23]. In particular, the combination of warming and habitat contraction, caused by dam construction, has resulted in large population declines and erosion of salmon life history diversity, particularly for runs that rely on cooler high-elevation habitats[18,24–26]. To understand how life history diversity may influence salmon resilience to climate change, we tracked the relative contribution of different juvenile migratory strategies in California's Chinook salmon (*Oncorhynchus tshawytscha*) populations that spawn in a heavily modified environment at the southern edge of the species' native range[27]. These salmon serve as a model system for early indication of the challenges faced by cold-water fishes when access to thermal refugia has been drastically reduced[28].

While juvenile salmonids at higher latitudes often spend many years in freshwater before emigrating to the ocean[27,29], today, most salmon in the California Central Valley emigrate in their first winter or spring before river temperatures become too warm. An exception is found among spring-run Chinook salmon that used to dominate the region before the construction of impassable dams[24]. Two populations still have access to high elevation reaches and exhibit a now-rare phenotype where juveniles remain in the river over summer before emigrating the following fall[30]. This late-migrating phenotype relies on access to cool water for the entire rearing period and is therefore most likely to be negatively impacted by warming temperatures and impaired access to high-elevation reaches. Here, we used strontium isotope ratios ($^{87}Sr/^{86}Sr$) and daily depositional chronology in otoliths (calcium carbonate structures, part of the fish's hearing and balance system) to reconstruct the juvenile emigration patterns and growth rates of returning (that is, successful) adult spring-run Chinook salmon, and to estimate the contribution of different migration strategies to the reproductive population across environmental extremes. Specifically, $^{87}Sr/^{86}Sr$ varies among California Central Valley rivers, producing distinct and reproducible geographic markers across the landscape that are permanently recorded in the daily otolith layers, thus allowing reconstruction of the juvenile life histories of 123 adults that returned to Mill and Deer Creeks (two geographically close watersheds with genetically similar spring-run populations[31]; Fig. 1a) between 2007 and 2018 (Supplementary Table 1). Some of these cohorts experienced severe droughts and warm ocean conditions (Supplementary Table 2)

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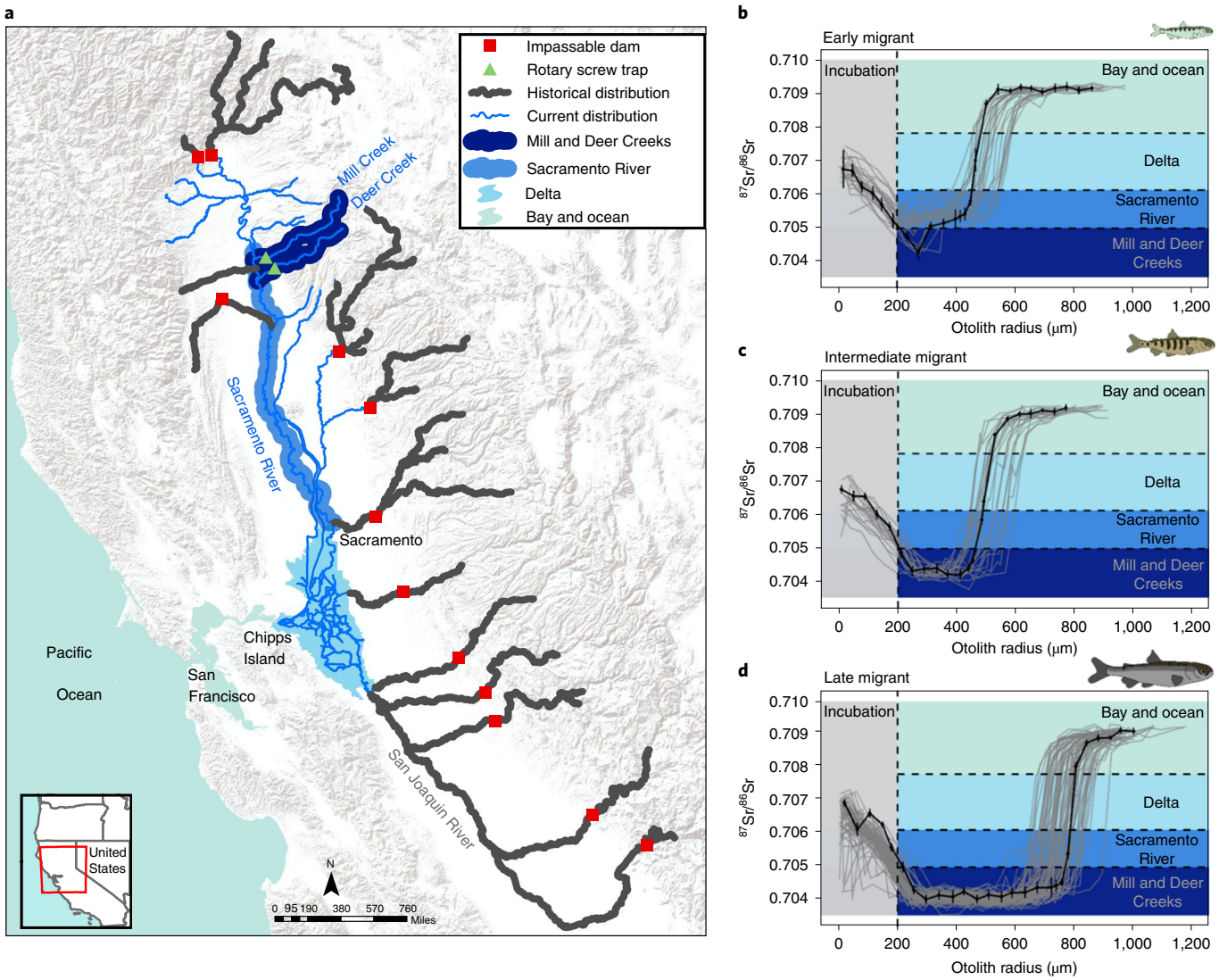


**Fig. 1 | Spring-run Chinook salmon life history diversity. a**, Map of historical and current distribution of California Central Valley spring-run Chinook salmon, with the two Lassen tributary populations in this study highlighted in dark blue. Delta, Sacramento–San Joaquin River Delta; Bay, estuary between Suisun and San Francisco Bays; and Chipps Island, freshwater exit location. **b**–**d**, Otolith strontium isotope profiles (grey lines) separated into early (**b**), intermediate (**c**) and late migrants (**d**). Life history types were classified using cluster analyses based on otolith isotope-by-radius data for all years combined (Methods and section 1.2 in the Supplementary Information). A representative profile from each cluster (±2 s.d.) is shown in bold. The first part of the profile (0 to ~200 μm; represented by a grey rectangle) corresponds to the incubation period when the fry is nourished by the maternal yolk in the gravel. **a**, Credit: Esri, USGS, NOAA.

revealing potential mechanisms involved in the expression and success of alternative life history strategies. We also investigated how predicted future river temperatures will affect the availability of suitable rearing habitat and the long-term viability of the late-migrating phenotype. In summary, we show how climate change may truncate salmon life history diversity and how the loss of the late-migrant phenotype could negatively affect the long-term resilience of threatened spring-run Chinook salmon populations.

## The importance of rare phenotypes and life history diversity

Otolith isotope profiles revealed three distinct juvenile life history types (hereafter referred to as 'early', 'intermediate' and 'late' migrants; Fig. 1b–d and Supplementary Fig. 1), concordant with the three emigration modes observed in the juvenile trapping data (Fig. 2a). The three life history types were characterized by significant differences in the age and size at which the fish exited the natal tributary (Figs. 1b–d and 2b and Supplementary Fig. 2c,e). Despite leaving the natal stream considerably smaller, early migrants entered the ocean at a similar size and age to intermediate migrants, after rearing for multiple months in non-natal freshwater habitats (that is, Sacramento River and Delta). Late migrants emigrated to the ocean significantly later and larger than the other two phenotypes (Fig. 2c and Supplementary Fig. 2d,f), having reared in the natal stream over the summer (mean natal rearing period, 194 ± 32 d). Late migrants may thus experience very different freshwater, estuarine and nearshore marine conditions, potentially resulting in differential feeding, growth and survival opportunities[32,33].

While late migrants were the rarest phenotype (10%) observed in juvenile monitoring traps[34], they represented most (60%) of the returning adults averaged across years (Fig. 2a,b). Conversely, on average, 26% of juveniles and 19% of surviving adults were

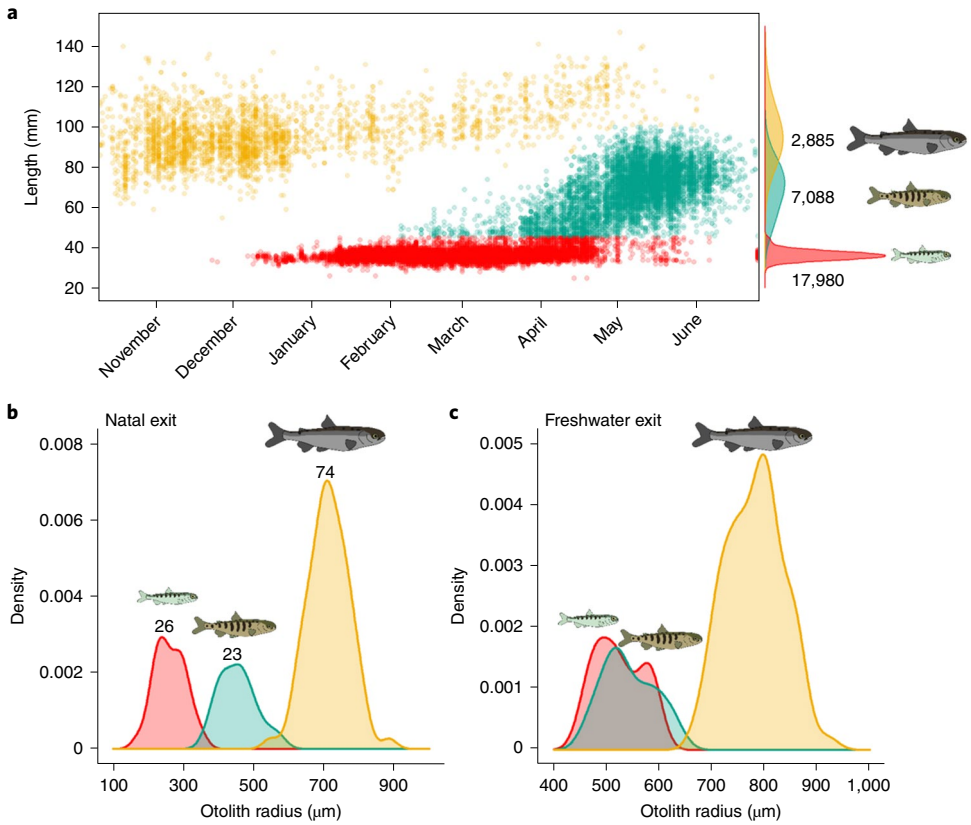


**Fig. 2 | Migrant size distributions at natal and freshwater exit. a**, Raw catch data and size distribution of juveniles caught in the Mill and Deer Creek rotary screw traps between 1995 and 2010. Each colour represents a life history type on the basis of its size and date at emigration: red, early; green, intermediate; and yellow, late migrants (section 2.1 in the Supplementary Information). Numbers near each density profile represent fish counts per life history type. **b**,**c**, Otolith radius (proxy for fish size) distributions for each life history type showing when juveniles emigrated out of the natal stream (**b**) and out of freshwater (**c**). Colours correspond to life history types denoted in Fig. 1. Numbers above each density peak represent fish counts per life history type. Note that the juvenile emigration years associated with return years from the otolith analysis (2004–2015; Supplementary Table 2) do not entirely match with the emigration years from juvenile trapping data (monitoring performed from 1995 to 2010).

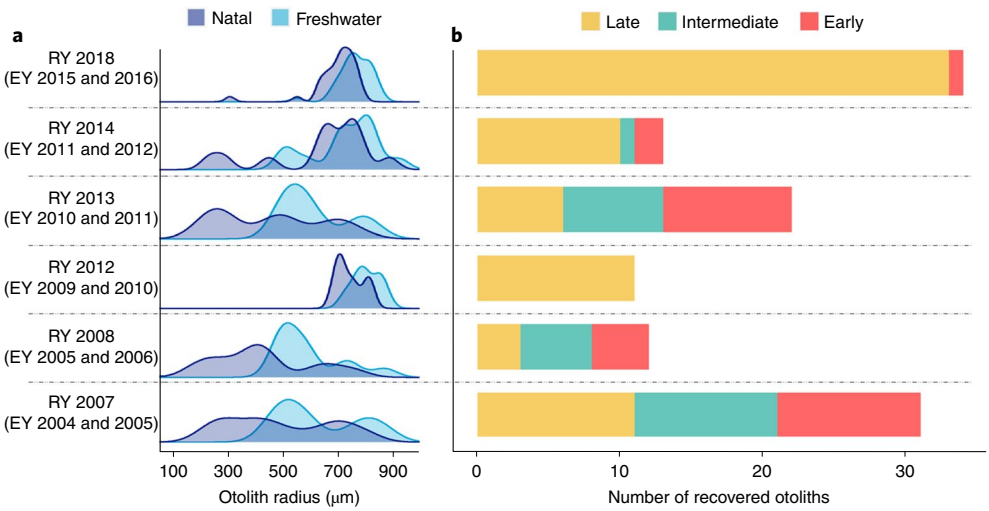


**Fig. 3 | Migrant sizes and life history diversity across years. a**, Otolith radius (proxy for juvenile fish size) distributions for each adult return year (RY) and its most likely juvenile emigration years (EY, shown in parenthesis) at natal and freshwater exit, showing interannual differences in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

represented by intermediate migrants that reared in natal rivers for $84 \pm 27$ d. Early migrants, that reared in natal rivers for $15 \pm 14$ d, were the dominant phenotype observed in juvenile monitoring (64%), yet their contribution to the adult returns was suppressed (only 21%). Importantly, the contribution rate of each life history type varied considerably among years (Fig. 3). Half of the return

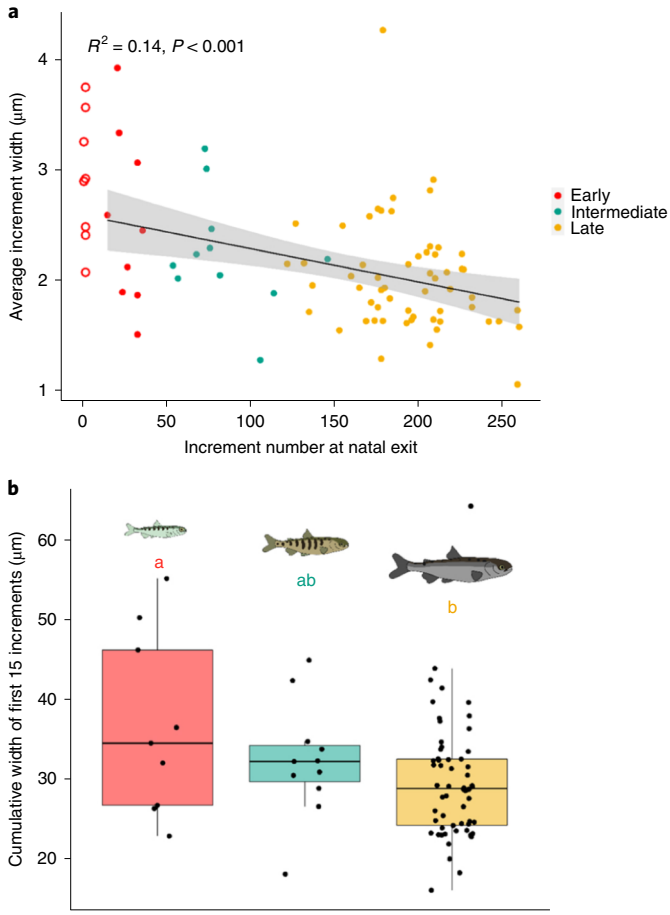


**Fig. 4 | Early-life salmon growth across life history types. a**, Fish daily otolith increment width (a proxy for fish growth rate) averaged over the first 15 d after emergence and plotted against the otolith increment number (a proxy for age in days) at natal exit, for each life history type. Filled circles show individuals that were still in their natal tributary at day 15 and used for the early-life growth analysis, while open circles represent individuals that had left their natal tributary before day 15 and reared elsewhere. A linear regression is represented by the black line, with the grey shade showing the 95% confidence interval. Even excluding the fast-growing individuals (open circles), there is a negative relationship ($R^2$ and $P$ value) between age at natal exit and initial growth rates. **b**, Boxplot comparing cumulative increment width at day 15 (a proxy for somatic growth achieved in the first 15 d) between the three migratory phenotypes. Only fish that spent at least 15 d in the natal stream were included. The horizontal line in each box represents the median value, lower and upper hinges of the boxes correspond to the 25th and 75th percentiles. The upper whiskers extend from the hinge to the largest value no further than 1.5 × interquartile range (IQR) from the hinge. The lower whisker extends from the hinge to the smallest value, 1.5 × IQR of the hinge, at most. The black dots are the actual measurements. Boxes not sharing the same letter are significantly different (Tukey test with significance level $\alpha = 0.05$, d.f. = 75).

years (2007, 2008 and 2013) were represented by similar contributions of each life history type, and their most likely emigration years (2004 and 2005, 2005 and 2006, 2009 and 2010) were generally wetter. In contrast, the late migrants that left freshwater in the fall during multiyear droughts and ocean heatwaves (returning 2012, 2014 and 2018) were functionally the only strategy to survive to adulthood (100%, 77% and 97% of late migrants observed, respectively; Fig. 3 and Supplementary Table 2).

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

## Thermally suitable habitat in a warming climate

Temperature strongly influences salmonid physiology, growth and survival[36]. Thus, populations with access to diverse water temperatures during incubation and natal rearing are predicted to exhibit increased phenotypic and phenological diversity[37]. To support late migrants, stream temperatures need to remain suitably cool (temperature below ~15 °C; ref. [38]) over the summer to accommodate the extended rearing period. Mill and Deer Creek watersheds, along with upstream reaches of the Battle and Clear Creeks, are among the few accessible and populated spring-run streams in the system that still provide suitable rearing temperatures to support all three phenotypes (Fig. 5 top panels). In accessible stream reaches where spring-run Chinook were historically present but are now extirpated, only the Stanislaus River has temperatures that could support the late-migrating phenotype. Adult spring-run Chinook (based on return timing) have recently been observed in the Stanislaus River suggesting that this habitat has the potential to support recolonization thus contributing to the reintroduction efforts in the San Joaquin Basin[39]. Importantly, increases in spring and summer stream temperatures by 2040 (Extended Data Fig. 1) and 2080 (Fig. 5 bottom panels) are predicted to further contract the amount of thermally suitable rearing habitat, especially along the downstream reaches of spring-run streams and the mainstem Sacramento River. Without intervention, late migrants may only have access to 76 km of suitable summer rearing habitat by 2080, less than half (44%) of the accessible suitable habitat during our study period (that is, 2005–2015; Supplementary Table 3). Providing access above dams on the Sacramento, Feather, Yuba, American and Tuolumne Rivers (Fig. 5) would approximately triple summer rearing habitat under 2080 climate conditions (76 km without access, 201 km with access; Supplementary Table 3).

## Discussion

Here, using archived otolith tissues, we reveal how a diversity of growth rates and behaviours expressed during early life stages can shape population dynamics and resilience via within-population portfolio effects. This underscores why it is essential that conservation strategies developed for the recovery of vulnerable species support both rare and common phenotypes. The phenotypic diversity expressed by California Central Valley spring-run Chinook salmon has thus far enabled these populations to persist despite habitat loss and degradation along their migratory corridor, warming temperatures and an increasingly volatile Mediterranean climate[24,40]. We show for the first time that the late-migrating strategy is the life-support for these populations during current periods of extreme warming. Therefore, conservation priorities should focus on supporting this rare and climate-adapted behaviour, particularly given that climatic extremes such as extended droughts and marine

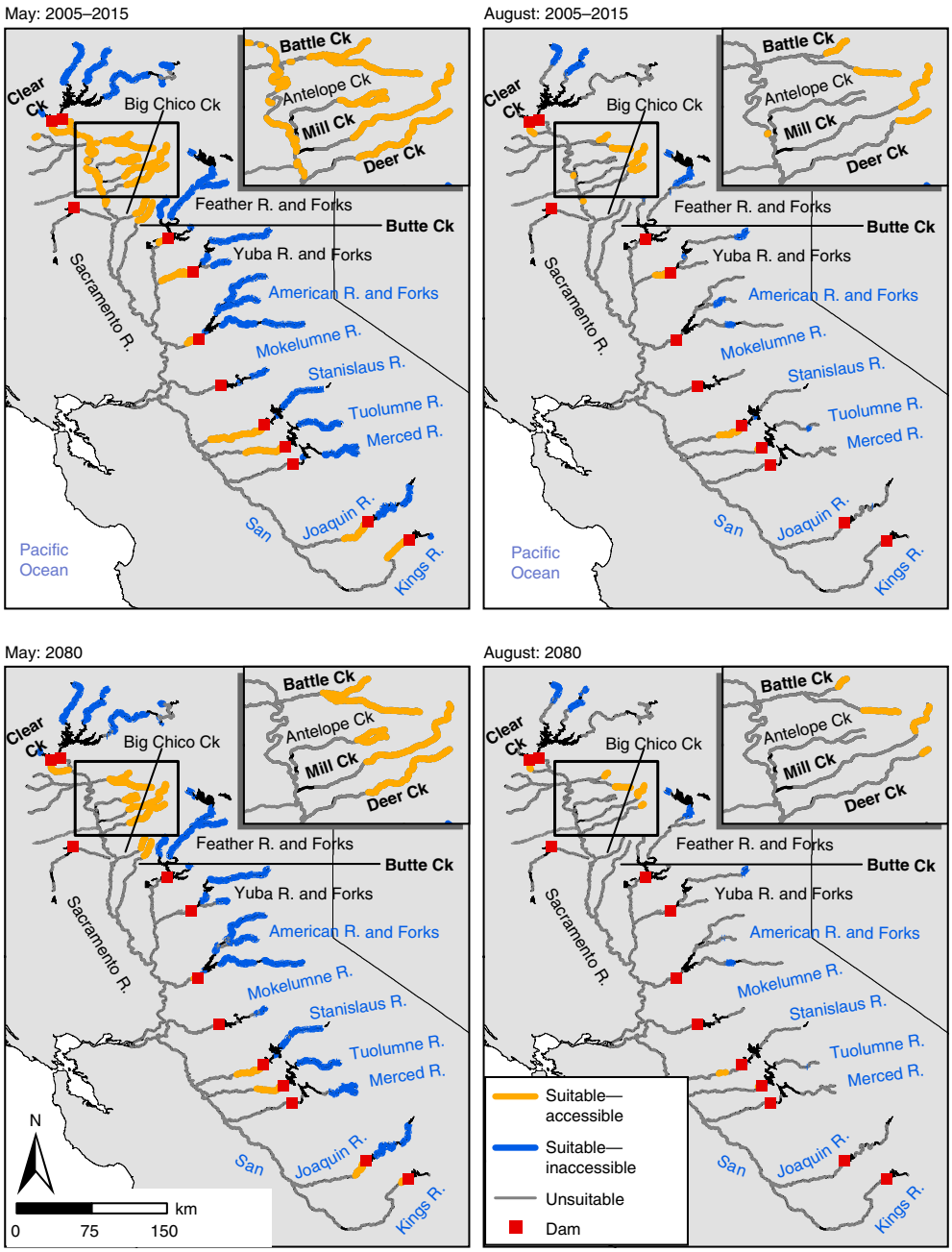


**Fig. 5 | Central Valley habitat suitability mapping under current and future climate conditions.** Rearing temperature suitability (temperature <15 °C; ref. [38]) in accessible (orange lines) and inaccessible (that is, blocked by impassable dam; blue lines) river reaches in the California Central Valley, focusing on months when temperature stress is most likely to impact rearing success for early and intermediate migrants (May; left panels) and late migrants (August; right panels). We examined suitability (defined as temperature <15 °C; Methods) during our study period (top panels) and under a future climate change scenario (2080, bottom panels). The inset maps highlight our study streams (Mill and Deer Creeks) and nearby spring-run streams. Major current and historical spring-run streams are labelled, with extirpated populations in blue font, and populations at low risk of extirpation[56] in bold. The grey lines represent reaches that are thermally unsuitable for rearing (mean monthly temperature >15 °C). The black lines represent reaches where temperatures could not be predicted reliably (for example, reservoirs). See Methods for details on temperature mapping. R., River; Ck, Creek.

heatwaves are predicted to increase in frequency and severity in the future[41,42]. Late migrants experience very different selective pressures to the other migratory phenotypes, during both their freshwater and ocean phases. For example, entering the ocean in a different season at a larger size potentially reduces intraspecific competition and risk of mismatch with peak prey production during early ocean residence, a critical period for cohort success[43]. However, by rearing over summer in freshwater late migrants forgo growth opportunities that early and intermediate migrants experience by feeding earlier in the more productive ocean. This within-population phenotypic diversity is thus critical to spreading risk and ensuring that at least some fraction of the population is successful under differing environmental conditions.

For salmon and other species impacted by habitat contraction, restoring and maintaining a diverse mosaic of habitats and thermal refugia across the freshwater landscape will be critical

to support life history diversity and long-term persistence[22]. For spring-run Chinook salmon, predicted stream temperatures under our climate change scenarios demonstrate the necessity for maintaining and expanding thermally suitable rearing habitat to support diverse growth rates and a broad spread of emigration timings. Juvenile salmon in the Central Valley are known to experience high mortality rates during their seaward migration in the spring particularly during droughts[44,45]. This is further evidenced by the poor representation of early and intermediate migrants in the adult returns in 2012, 2014 and 2018, which were all characterized by hot and dry emigration conditions. Late migrants have evolved a drought-resilient strategy of leaving in the fall when the migratory corridor is cooler but they must be able to survive the heat of the spring and summer in headwater habitats for this to be a viable strategy. Improving access to cold-water refugia through habitat restoration, targeted water management below dams and/or reintroductions to high-elevation habitats above impassable dams, might be vital for preserving the late-migrant life history type now and under future climate scenarios[46,47]. While the predicted amount of summer rearing habitat above dams may be modest under 2080 conditions (125 km; Supplementary Table 3), this reliable cold water could play a disproportionate role in preventing extirpation during multiyear droughts. In addition, improving growth and survival conditions for early and intermediate migrants along degraded migratory corridors could be instrumental to bolster productivity and resilience, particularly in wetter years when earlier migrants play an important role in population success.

Salmonid species are renowned for their extensive migratory plasticity, with anadromous forms spending a few months to many years in freshwater[48]. While phenotypic trait diversity in salmon species is often discussed in the context of genetic differentiation and microevolution[49,50], the life history diversity observed in these genetically similar spring-run populations[31] highlights the important interaction between physiology and environmental variability in the expression of divergent juvenile emigration strategies[51]. Although physiological plasticity can increase species' resilience to climate change[52], it is unclear whether salmonids can adapt their thermal tolerances quickly enough to keep pace with predicted rates of warming. This is particularly problematic for populations at lower latitudes[53] and those facing additional stressors (for example, contaminant loads, limited food) that further contract their thermal window by affecting their metabolic performance[54]. As environmental conditions continue to shift rapidly with climate change, maximizing habitat options across the landscape to enhance adaptive capacity and support climate-resilient behaviours may be crucial to prevent extinction events within salmonids and other thermally vulnerable species[23,52,55].

## Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-021-01186-4.

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## Methods

**Otolith $^{87}Sr/^{86}Sr$ analysis.** Otoliths were prepared at UC Davis per established techniques[57]. The otoliths' sagittal plane (see Fig. 3 in Woodson et al.[32]) was sectioned on both sides using 600 and 1,500 grit wet/dry sandpaper to expose the primordia and surrounding microstructure. The surface achieved a further fine polish using 3 and 1 μm $Al_2O_3$ lapping films. Finished samples were mounted to a 1 $cm^2$ glass pedestal using Gorilla Glue. The otoliths' dorsal side was photographed in ×20 magnification using a Qimaging digital camera (MicroPublisher 5.0 RTV) mounted to an Olympus BX60 microscope. Following imaging, otoliths were analysed for strontium isotopes at the UC Davis Interdisciplinary Center for Inductively Coupled Plasma Mass Spectrometry by laser ablation on their Multi Collector Inductively Coupled Mass Spectrometer. We used the otolith strontium isotope methods described in Barnett-Johnson et al.[58,59] to reconstruct juvenile freshwater habitat-use and migration histories. In brief, the strontium isotope ratio ($^{87}Sr/^{86}Sr$) of freshwater habitats (the 'isoscape') varies as a function of rock geology and weathering patterns[60] and, because there is no biological fractionation of strontium isotopes, the otoliths faithfully record the signature of the surrounding water and dietary sources. Strontium isotopes are a particularly powerful tool in the California Central Valley, because the spatial heterogeneity in rock types results in significant differences in isotope signatures among most of the salmon-bearing watersheds. Consequently, variations in $^{87}Sr/^{86}Sr$ and strontium concentration across Central Valley watersheds has proven useful for determining population of origin[59,61] and reconstructing juvenile rearing and migration behaviour[44,62].

**Movement reconstruction.** Otolith radius was used as a proxy for fish size at natal and freshwater exit (section 2.2 in the Supplementary Information). The otolith radius for each $^{87}Sr/^{86}Sr$ measurement was estimated by measuring the distance from the otolith core to the centre of each laser pit along a standardized 90° axis[57]. Strontium isotope profiles representing changes in $^{87}Sr/^{86}Sr$ values as a function of otolith distance from the core were created for each otolith. Specific location $^{87}Sr/^{86}Sr$ threshold values were used to identify the movement of Central Valley spring-run Chinook juveniles from one rearing region to the other. These values come from a Central Valley isoscape database[62]. We considered four distinct regions in this study: Natal tributary (Mill and Deer Creeks), Sacramento River, Sacramento–San Joaquin Delta (hereafter 'Delta') and San Francisco–San Pablo Bay (hereafter 'Bay') and Ocean. We used changes in $^{87}Sr/^{86}Sr$ along the otolith transect to identify two key habitat shifts to reconstruct the size at which individuals exited (1) the natal tributary and (2) freshwater (exit location is Chipps Island, river-km 73). Otolith radius at natal exit was calculated by linearly interpolating between otolith distances at the $^{87}Sr/^{86}Sr$ measurements on either side of the upper Sacramento River (point of Mill and Deer Creek exit and Sacramento River entry) strontium threshold value. We used the lowest $^{87}Sr/^{86}Sr$ value found for the upper Sacramento River region in the Central Valley isoscape database. If, for a given fish, this threshold was never crossed (that is, $^{87}Sr/^{86}Sr$ values are all above the threshold), we determined it by visually identifying the closest point to the Mill/Deer Creek habitat $^{87}Sr/^{86}Sr$ threshold value in the strontium profiles. This could happen if a fish migrated quickly after emergence to the Sacramento River, which is characterized by higher $^{87}Sr/^{86}Sr$ values than the natal tributary. Similarly, otolith radius for freshwater exit was calculated by linearly interpolating between otolith distances at the $^{87}Sr/^{86}Sr$ measurements on either side of the Chipps Island (point of Delta exit and Bay entry) strontium threshold value. Finally, the Sacramento River at Freeport $^{87}Sr/^{86}Sr$ value threshold was used to identify the migration of spring-run juveniles from the mainstem Sacramento River to the Delta.

**Clustering analysis.** We conducted a clustering analysis[63] on the strontium profiles obtained from the otolith microchemistry analysis to investigate whether we could statistically identify groups of fish exhibiting similar juvenile rearing strategies among Mill and Deer Creek populations. Strontium profiles were considered as smooth curves or functions sampled at a finite subset of some interval (here, the distance from the otolith core); the statistical methods for analysing such data are described as 'functional data Analysis' (FDA; see Ramsay and Silverman[64] for an overview of FDA). With FDA methods each profile is modelled in an infinite functional space rather than considered as a discrete vector in a multidimensional space (as modelled in multivariate data analysis). The clustering analysis performed in this paper included the following steps:

(1) A smoothing spline was fitted to each profile to predict continuous $^{87}Sr/^{86}Sr$ values for otolith radius distances between 0 and 1,000 μm (using the smooth.spline function in R; ref. [65]). This allows us to obtain a smooth version of the profiles for any distance from the otolith core to 1,000 μm so that a direct comparison of all Mill and Deer Creek strontium profiles of different lengths can be achieved.
(2) Each smoothed profile was then transformed into a functional data object (that is, decomposed in terms of linear combinations of known basis functions), using a B-splines basis (using the fda package in R; ref. [64]).
(3) A functional principal component analysis was performed on those functional objects (using fda package in R). This allowed us to identify the principal modes of variation of the functional dataset and reduce data dimensions which has been shown to help for clustering pattern recognition and processing time[63].
(4) We used a model-based clustering method, where the data were represented by a series of Gaussian mixture models for which each point (that is, each profile) was associated with a probability of belonging to each potential cluster[66]. The mixture model parameters were estimated using the expectation-maximization algorithm.
(5) The Bayesian information criterion was used to select the best model with the optimal number of clusters (using mclust package in R; ref. [67]).

**Early-life growth rate estimation.** To estimate habitat-specific juvenile growth rates we measured the otolith increment widths using Image Pro Premier 9.0 (Media Cybernetics) in each isotopically distinct habitat region[57]. Each otolith reading was assigned a score of 'certainty' on a scale of 1–5: 1, unusable; 2, hard to read the majority of increments; 3, hard to read some of the increments; 4; easy read; and 5; perfect publication quality. This index is a combination of the reader's confidence in the accuracy of the increment placement and the quality or readability of the image (that is, how likely it is that another reader would get the exact same increment width measurements). Otoliths with poor readability (with a score of 3 or lower) were eliminated from the analysis. A total of 86 otoliths were used for growth rate estimations.

**Central Valley spring-run streams temperature suitability mapping.** To explore why Deer and Mill Creeks may exhibit multiple juvenile life histories and how life history expression may change with climate change, we compared current and future thermal conditions along every current and historical spring-run stream. Temperature was obtained from a mean monthly stream temperature model[20]. In brief, FitzGerald et al.[20] used a spatial stream temperature model to predict mean monthly stream temperature for nearly every river-km in the western United States. In the Central Valley, the test sample $r^2$ was 0.813 and the mean absolute prediction error (MAPE) was 1.024 °C. We first clipped this stream temperature dataset with the current and historical Central Valley spring-run distributions[68]. In general, the distribution and stream networks matched but a few reaches with spring-run did not have stream temperature. We averaged the monthly temperature at each stream segment from 2005 to 2015, representing our study period. In the Central Valley, stream temperatures are predicted to increase by 0.6 °C by 2040 and 1.0 °C by 2080[69], so we applied these deltas to the temperature dataset.

We then examined stream temperature suitability for juveniles rearing in May and August of 2005–2015, 2040 and 2080. We focused on months when temperature stress is most likely to impact rearing success for early and intermediate migrants (May) and late migrants (August). A river reach was defined as suitable when it provided optimal temperature for spring-run juvenile growth. Here, we used a fixed temperature threshold of 15 °C because temperatures greater than ~15 °C result in decreased growth rates and increased mortality rates, yet we acknowledge that there is probably some variation in this threshold according to local water quality, food availability and the life stage considered[54,70].

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

## Data availability

The datasets generated and used for the otolith strontium isotope and early-life freshwater growth analyses and to produce Figs. 1–4 and Supplementary Figs. 1–3 are available on GitHub at https://github.com/floracordoleani/MillDeerOtolithPaper (ref. [71]). The stream temperature and spring-run Chinook spatial distribution shapefiles generated for the juvenile spring-run Chinook thermal habitat suitability assessment and used in Fig. 5, Extended Data Fig. 1 and Supplementary Fig. 4 are available on DRYAD at https://doi.org/10.5061/dryad.bk3j9kdc9 (ref. [72]).

## Code availability

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

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## Author contributions

F.C., C.C.P., P.K.W., A.M.S. and R.C.J. conceived the study. F.C. led data collection and analyses. F.C., C.C.P., A.M.S., A.M.F., P.K.W., A.M. and R.C.J. contributed to data analyses and manuscript writing. G.E.W., C.C.P. and P.K.W. conducted the otolith microchemistry and microstructure analyses. A.M.F. performed the temperature prediction modelling and A.M. performed the clustering analysis.

## Competing interests

The authors declare no competing interests.

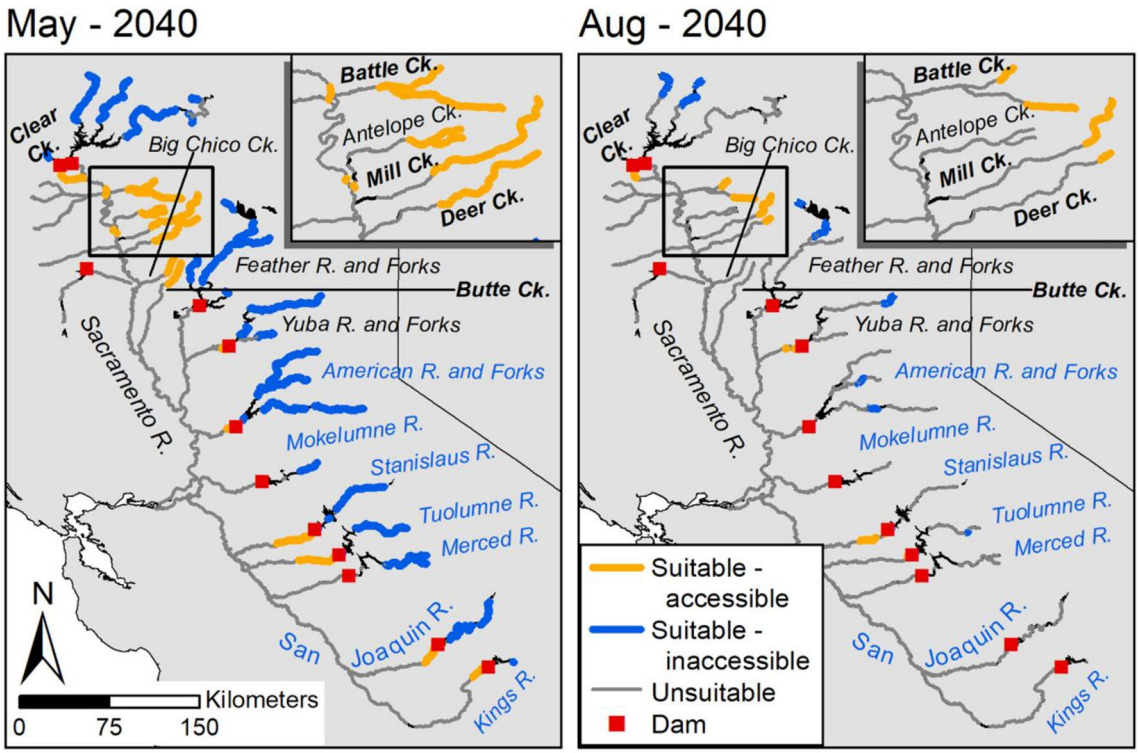
## Additional information

**Extended data** is available for this paper at https://doi.org/10.1038/s41558-021-01186-4.

**Supplementary information** The online version contains supplementary material available at https://doi.org/10.1038/s41558-021-01186-4.

**Correspondence and requests for materials** should be addressed to F. Cordoleani.

**Peer review information** *Nature Climate Change* thanks Rebecca Buchanan, Daniel Schindler and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.




**Extended Data Fig. 1 | Central Valley habitat suitability mapping under a climate change scenario for 2040.** Details of this figure are identical to Fig. 5, except displayed for 0.6 °C stream temperature increase.

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## Software and code

Policy information about availability of computer code

| | |
|---|---|
| Data collection | Pro Premier 9.0 software (Media Cybernetics) was used to collect otolith growth increment data. |
| Data analysis | We used R statistical language version 4.0.2 for the otolith strontium isotope and early life growth analyses and the codes are available on Github at https://github.com/floracordoleani/MillDeerOtolithPaper. The juvenile spring-run Chinook Salmon thermal habitat suitability assessment was performed the stream temperature model from Isaac et al. 2017 and ArcGis. This analysis was similar to the one performed by FitzGerald et al. 2020 but considering a narrower region (i.e. only spring-run distributions in the California Central Valley) and the juvenile rearing life stage only. |

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

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# Ecological, evolutionary & environmental sciences study design

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| | |
|---|---|
| Study description | We reconstructed the juvenile life histories of 123 spring Chinook salmon adults that returned to Mill and Deer Creeks between 2007 and 2018 using otolith strontium isotope analysis. The early-life freshwater growth rates were also estimated for those fish by conducting an otolith increment analysis and growth rate differences were associated with the different life history types identified through the isotope analysis. Finally, we used a stream temperature model to investigate how present Central Valley river temperatures (from 2005-2015) and predicted future temperatures in 2040 and 2080 may affect the availability of suitable rearing habitat for spring run Chinook salmon juveniles and truncate the spring run populations life history diversity. |
| Research sample | We studied California Central Valley's Mill and Deer Creek spring-run Chinook Salmon (Oncorhynchus tshawytscha) populations, which are two of the three wild self-sustained spring-run Chinook populations remaining in the Central Valley. Those fish are listed as threatened under the federal Endangered Species Act. |
| Sampling strategy | We used all Mill and Deer Creek spring run adult otoliths that were collected between 2007 and 2018 by the California Department of Fish and Wildlife from adult carcasses after they naturally died following spawning. While we did not have any control on the amount of otoliths provided by CDFW we quantified the joint confidence intervals for the proportion of each life history type found within a year and we believe that our sample size was sufficient to give a good representation of the life history diversity observed among spring run Chinook salmon juveniles (i.e. the year to year differences in life history type proportions we observed are true differences and not artifacts of the sample size). |
| Data collection | The otolith strontium isotope and increments data were collected by George Whitman from UC Davis. The otoliths' sagittal plane was sectioned on both sides using 600 and 1500 grit wet/dry sandpaper to expose the primordia and surrounding microstructure. The surface achieved a further fine polish using 3µm and 1 µm Al2O3 lapping films. Finished samples were mounted to a 1cm square glass pedestal using Gorilla GlueTM. The otoliths' dorsal side was photographed in 20x magnification using a Qimaging digital camera (MicroPublisher 5.0 RTV) mounted to a Olympus BX60 microscope. Daily otoliths growth increments were measured and counted along a standardized 90° transect using Image Pro Premier 9.0.otoliths. Otolith trontium isotope ratios were measured from the core to the edge of each tolith along the same standardized 90° transect at the UC Davis Interdisciplinary Center for Inductively-Coupled Plasma Mass Spectrometry by Laser Ablation on their Multi Collector Inductively Coupled Mass Spectrometer. |
| Timing and spatial scale | The otoliths were collected in both Mill and Deer Creek spawning ground every summer during the carcass surveys. The otolith growth analysis was performed first and the strontium isotope analysis was performed when UC Davis laser was available. This lasted several months. |
| Data exclusions | Otoliths that broke during the preparation phase were eliminated from the strontium isotope analysis. A total of 123 otoliths were used. Additionally, each otolith increments reading was assigned a score of "certainty" on a scale of 1-5, 5 being the highest certainty. This index is a combination of the reader's confidence in the accuracy of the increment placement and the quality or readability of the image (i.e., how likely it is that another reader would get the exact same increment width measurements). Otoliths that had poor readability were eliminated and a total of 86 otoliths were used for growth rate estimations. |
| Reproducibility | Within each isotope analysis of otolith samples on a petrographic slide (6-8 samples), measurements are made on the edge of each otolith (marine) as well as known ocean carbonate standards are measured before and after each slide to ensure the calibration accuracy of the instrument for each set of 6-8 samples.<br>Among-reader precision and accuracy was estimated by performing multiple increment reads on a sample of otoliths. Among-reader precision, calculated as the average coefficient of variation for multiple reads of the same otolith by 2-4 independent readers, was 6.2% which is well within optimal reproducibility for age and growth laboratories (Campana and Thorrold 2001). The mean difference between estimated versus known age of juveniles was 0.2 days (mean absolute difference of 2.4 days), based on reads performed by 2-4 independent readers which suggests high reproducibility. |
| Randomization | Otolith samples were randomly assigned to petrographic slides regardless of the year they were collected to reduce spurious artifacts of potential variation in instrument performance resulting in a "year effect". |
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