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Title: Does fine-scale habitat diversity promote meaningful phenotypic diversity within a watershed network?

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Life history diversity facilitates long-term species persistence by buffering populations against environmental stochasticity across space and time (Schindler et al. 2010). In California, numerous salmonid species are declining precipitously, with nearly 75% expected to be extirpated by 2100 (Moyle et al. 2017). Conservation of these imperiled species relies, in part, on conserving (i) remaining habitat heterogeneity and (ii) population life history diversity in a rapidly changing landscape. Recent research suggests that volcanic spring-fed rivers may fulfill both objectives. Spring-fed ecosystems are both physically and biologically distinct from the more abundant runoff rivers found throughout the greater Pacific Northwest (Lusardi et al. 2016). While numerous geophysical and biological processes have been documented in spring-fed streams, there is generally a paucity of information about how these differences in environmental variables translate to top consumers. Thus, documenting differences in key life history traits of a top predator between spring-fed and runoff rivers within a stream network and understanding how these life histories relate to their different habitats would provide information needed to assess the ecological value of spring-fed habitats with respect to the long-term persistence of species. Here, we describe differences in growth and life history timing between two distinct populations of native resident rainbow trout (*Oncorhynchus mykiss*) from spring-fed and runoff rivers located within the same watershed in northern California.

We sampled two distinct populations of *O. mykiss* from the upper Sacramento River Basin during fall 2018. The Upper Sacramento River Basin is divided into two geologic provinces including the Cascade Range in the eastern part of the basin and Klamath Mountains in the west. Hat Creek is a volcanic spring-fed stream in the eastern

part of the basin originating from young volcanic rock (e.g., andesites and basalts) associated with the Cascade Range Province. Here, snowmelt infiltrates into deep subsurface groundwater flow paths, eventually emerging as large springs. Conversely, Castle Creek occurs in the western basin which is composed of sedimentary and metamorphic rock that encourages snowmelt to runoff as overland and shallow subsurface flow. Using a backpack electrofisher, we sampled populations of wild 0⁺ *O. mykiss* from each stream. Individual fish were measured, weighed, photographed, and returned to the laboratory for otolith (ear stones) processing. Individual fish were dissected, and sagittal otoliths removed and polished in the sagittal plane to reveal daily growth increments. Increment counts and widths were measured beginning at the hatch check, whereas daily increment distances were measured from the primordia along a standardized dorsal transect to the edge (Barnett-Johnson et al. 2007).

Strikingly, 0⁺ *O. mykiss* from Hat Creek were, on average, 1.6-fold greater in length and 4.5-fold greater in mass compared to the 0⁺ cohort from Castle Creek (Figs. 1, 2a, 2b), which we hypothesize could be due to differences in growth and/or age of fish. Recent research suggests that secondary productivity associated with spring-fed rivers may be an important contributor to the growth of top predators, such as *O. mykiss*. For instance, Lusardi et al. (2020) found that prey availability was the predominant factor influencing differences in the growth of juvenile salmon in a spring-fed river when reared over a natural gradient of food resources and temperature. This suggests prey availability and, to a lesser extent, temperature has a strong influence on growth divergence between spring-fed and runoff river fish. Daily growth rates of otolith increments were significantly greater in the spring-fed cohort (Fig. 2d; repeated measures ANOVA, F=

24.8, $p < 0.0001$). However, such daily differences do not account for the entire length-mass discrepancies observed at capture. Indeed, most length and mass variability between spring-fed and runoff 0^+ *O. mykiss* was attributed to differences in egg emergence timing (Fig. 2c). On average, spring-fed *O. mykiss* emerged on March 25, 47 days earlier than runoff fish which emerged on average on May 10. Together, these data suggest that differences in daily growth and emergence timing contributed to the observed differences in length and mass at capture (Fig. 1).

We anticipate that there are inherent benefits to both attaining larger size and earlier emergence timing. Stream rearing is a critical phase in the early life history of salmonids and often determines the fate of a particular cohort (Armstrong et al. 2003). Einum and Fleming (1999) found that juveniles exhibiting size advantages experienced improved fitness in a stream environment and Williamson et al. (2010) found both size and age were positively correlated with salmonid fitness. For migratory salmonids, the implications may be even more important because early life stage growth and size can influence migration timing, size-selective survival, and competitive interactions (Woodson et al. 2013). Thus, volcanic spring-fed rivers, appear to confer a substantial growth advantage to juvenile salmonids. This suggests that these systems can strongly contribute to persistence of such populations, and, thus, represent important strongholds for recovery.

Previous research on life history diversity has focused on variation in the use of different broad-scale dominant habitat features such as lakes, rivers, floodplains, and lagoons which, together, create habitat mosaics that promote phenotypic diversity and population stability (Brennan et al. 2019). Our findings suggest, however, that particular

streams or hydro-environments at smaller spatial scales may represent important underappreciated features of riverscapes that are critical for creating and maintaining intraspecific diversity via evolutionary processes. For example, volcanic spring-fed rivers exhibit broad variability in numerous abiotic variables when compared with runoff systems (Lusardi et al. 2016, 2020). This suggests that these systems may be important in promoting life history and behavioral diversity within larger salmonid population complexes. Since our study only focused on two systems, it is possible that the differences observed could be related to other factors not measured nor specific to spring-fed or runoff rivers. For instance, it is possible that physiological (e.g., Shulte and Healy 2022) and (or) other ecological factors (e.g., relative density of fish between habitats, differences in predation intensity, or competition) may account for observed phenotypic differences between habitats. However, we posit that differences in discharge, temperature, nutrient availability, and habitat types, which are known to be consistently different between volcanic spring-fed and runoff rivers, result in divergent selection pressures, translating into diversified life history and behavioral adaptations for salmonids between systems.

The western United States is currently experiencing its worst drought in the last 1,200 years (Williams et al. 2022). As the climate continues to warm, the phenologies and distributions of many aquatic species are shifting; however, for numerous coldwater fishes, much of their remaining habitat is predicted to become increasingly compressed, unsuitable, or inaccessible due to barriers (Moyle et al. 2017). In the face of intensified warming and drought conditions, volcanic spring-fed rivers provide vital refuges for coldwater fishes and other biota that are otherwise likely to face climate-driven

extinctions (Swain et al. 2018). Spring-fed rivers throughout the Pacific Northwest buffer temperatures (e.g., warmer during winter and cooler during summer), dampen extreme flow events, and are less prone to intermittency during baseflow periods (Tague et al. 2007, Lusardi et al 2016). Conversely, runoff rivers are experiencing prolonged lower summer baseflow periods, increasing magnitude of winter flood events, earlier spring snowmelt, and marked increases in summer water temperature (Das et al. 2011, Null et al. 2013). Such differences between river types are associated with underlying geology, thereby emphasizing the linkages among physical habitat features, climate change, fish growth, phenology, and diversity in aquatic ecosystems (Tague et al. 2007, Lusardi et al. 2016).

Expanding on these observations is important, considering the implication of size and emergence differences with respect to portfolio effects (e.g., diverse populations or contributing to species complex stability through time; see Schindler et al. 2010, Brennan et al. 2019) and conservation of imperiled species. Foremost, our work suggests a need to explore differences in demographic measurements across multiple fish communities in other spring-fed rivers to determine the extent to which these results are repeatable. Such research may be particularly important in locations such as the Klamath River Basin, which is slated to have four major dams removed. Spring-fed rivers function as important habitats to anadromous fishes in the Klamath River (Wales 1963, Lusardi et al. 2018, 2020), so understanding how differences in size and emergence timing of salmonids translate into fitness, recolonization of historical habitat, and population stability is of high conservation value. Of other interest is understanding how differences in emergence timing and the onset of exogenous feeding (e.g., resource switching from

maternal yolk during the egg stage to aquatic invertebrates) in different river types are related to phenological shifts in prey abundance. While we anticipate that emergence timing and the onset of exogenous feeding have largely evolved as a developmental response to water temperature during egg incubation, it is also possible that differences in water temperature control phenological shifts in the abundance and density of invertebrate prey for foraging fishes (Anderson et al. 2019). By extension, adaptive processes that control spawn timing in salmonids may have evolved to coincide with prey availability for progeny and therefore may have a heritable component (Crozier et al. 2008). While this study does not examine the extent to which *O. mykiss* between these two systems are genetically different, further work is needed to understand linkages between genetic and environmental drivers of emergence timing. Given the enhanced productivity and year-round availability of prey in spring-fed systems (Lusardi et al. 2016), these data suggest there could be benefits associated with early emergence in spring-fed rivers. Therefore, understanding the relative contribution of water temperature and spawn timing on the emergence and ultimate success of juveniles between habitats is also of value.

The ecological literature suggests that broad-scale habitat diversity (e.g., lakes, floodplains, rivers) creates resilience in long-term salmon population dynamics and can play an important role in species diversity and persistence via the portfolio effect. Work presented here suggests that streams exhibiting different hydrologic regimes (e.g., groundwater or surface water dominated) also play an underappreciated role in promoting fish phenotypic diversity. Understanding how these differences manifest within the broader species complex is vital, considering the status of numerous freshwater fishes

globally. We suggest that identifying and prioritizing a deeper understanding of the role of environments whose effects on organisms are disproportionate to their abundance, i.e., “keystone environments”, will be fundamental to conservation and management.

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Authorship Contributions: RL, RD, CJ, and EVN conceived and designed the project. RL and CJ collected field specimens. GW and RJ dissected the specimens in the laboratory and prepped and analyzed otolith increments. RL drafted the initial manuscript which was critically revised by RD, CJ, EVN, GW, and RJ.

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Figure Captions

Figure 1. A) 0⁺ *O. mykiss* from Castle Creek (snowmelt runoff stream); weight: 2.53 g; length: 62 mm; estimated hatch date: May 17. B) 0⁺ *O. mykiss* from Hat Creek (volcanic spring-fed creek); weight: 24.9 g; length: 125 mm; estimate hatch date of February 23rd. Photographs taken by R. A. Lusardi.

Figure 2. Mean 0⁺ *O. mykiss* length (a) and mass (b) at time of capture (+ 1 standard error) and reconstructed otolith size for Castle Creek (run-off; red) and Hat Creek (spring-fed; blue) based on date (c) and age (d), based on back-calculated estimates from daily increment measurements with 95% confidence intervals of the lines in grey.

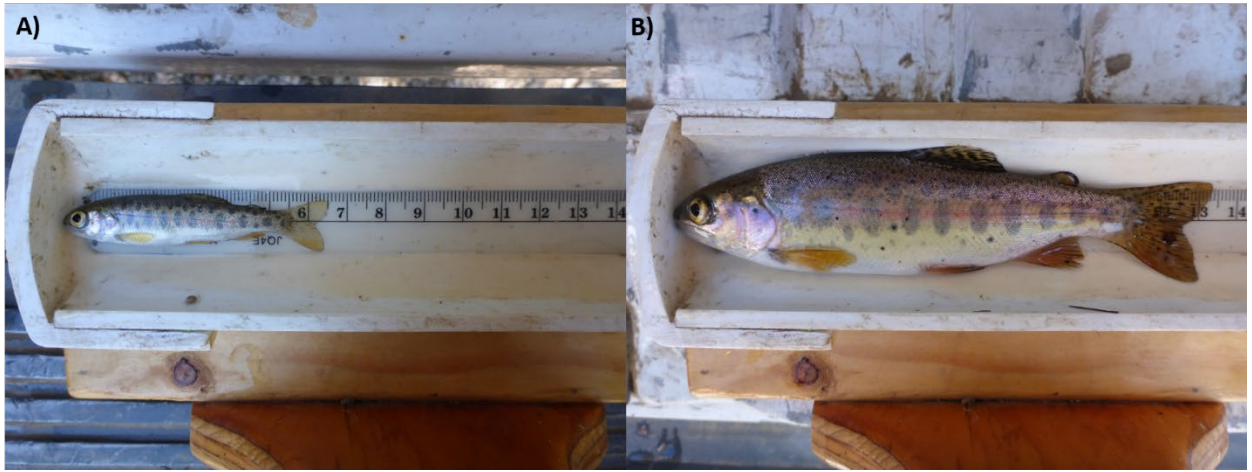


Figure 1

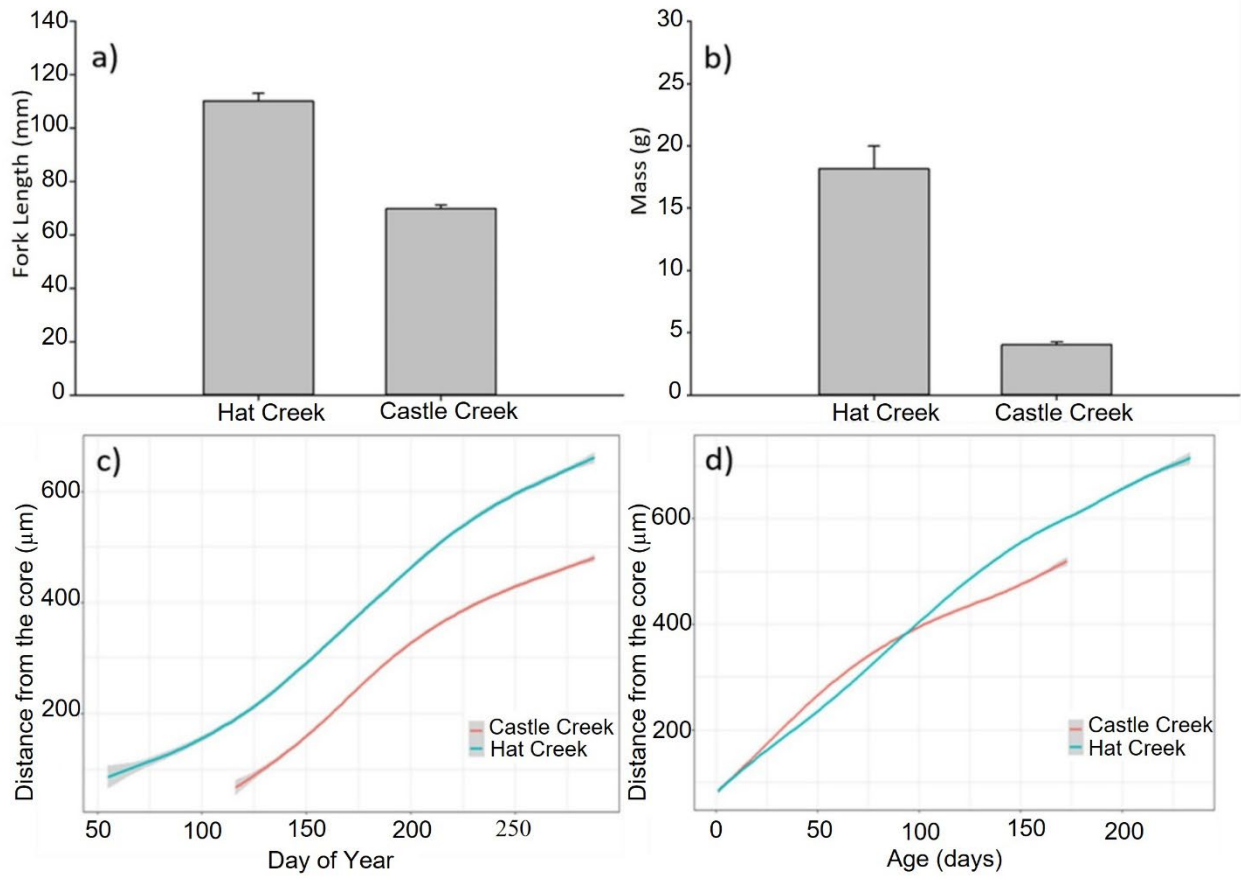


Figure 2