Review

Not All Rivers Are Created Equal: The Importance of Spring-Fed Rivers under a Changing Climate

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Abstract: In the Western United States, volcanic spring-fed rivers are anticipated to become increasingly more important for salmonids and other native fishes, as these rivers will retain coldwater habitats as the climate warms. Despite this, little is known about the hydro-biogeochemical interactions within these ecosystems. A review of existing literature on spring-fed rivers, coupled with a decade of research on volcanic spring-fed rivers of northern California, finds that these systems are exceptionally productive and exhibit stable environmental conditions. These unique conditions stem from hydrogeologic processes typical of young volcanic terrains. Aquatic macrophytes, common to some nutrient-rich spring-fed systems, play a disproportionate role in hydrologic and geomorphic processes by facilitating ecological interactions and velocity conditions that improve juvenile salmonid growth. We find that volcanic spring-fed rivers are also resilient to climate change, due not only to their ability to dampen water temperature changes through deep groundwater flow but also because of their nutrient-driven high ecosystem productivity, which may enable coldwater species to metabolically compensate for marginal increases in water temperature. Understanding the fundamental geomorphic and ecological differences between these rare ecosystems and their numerically dominant runoff rivers is essential for developing long-term conservation strategies for coldwater species under a rapidly changing climate.

Keywords: spring-fed rivers; coldwater fishes; climate change; conservation

1. Introduction

The loss of freshwater taxa has occurred at unprecedented rates [1,2]. In California alone, 74% of native salmonids are projected to be extirpated by 2100 [3] if present trends continue. Complicating matters, a 47% reduction in coldwater habitats is anticipated for many salmonids by 2080, as a result of climate change [4]. These projections suggest that productive and resilient habitats will play a more critical role in the future conservation of salmonids and other coldwater biota. However, our understanding of riverine processes that affect biodiversity, productivity, and distribution is limited to the types of systems most often studied in the geomorphic and ecological literature. Much of the literature regarding coldwater fishes, including salmonids, has focused on the physical, biological, and chemical processes associated with runoff-dominated rivers or those generating discharge from rain events and snowmelt (hereafter, runoff rivers or systems). This stems from the fact that runoff rivers are numerically dominant throughout western North America and elsewhere, are relatively common study systems, and are also anticipated to be strongly affected by climate change.

In contrast, volcanic spring-fed rivers, or those deriving discharge from groundwater and occurring in volcanic terrains, have received far less attention in the scientific literature [5,6]. These ecosystems exhibit a distinctive interplay between abiotic and biotic processes and are important contributors to coldwater fish production [7]. Most commonly, springs and spring-fed rivers are discussed in the context of their importance to aquatic biodiversity and rare macroinvertebrate or fish taxa (e.g., [8,9]), or are the subject of singular disciplinary studies focused on geomorphology or an individual trophic level (i.e., macroinvertebrates) within the broader food web (e.g., [10,11]). More recently, Cantonati et al. [12] discussed the need for a greater integrated understanding of springs and groundwater-dependent habitats and the species that depend on them. Thus, an interdisciplinary synthesis of the existing literature on volcanic spring-fed rivers and their importance in the context of conservation and climate change is strongly warranted.

Due, in part, to their voluminous spring accretions and lack of immediate reliance on precipitation, we anticipate that spring-fed rivers will play an increasingly important role in supporting coldwater biota in the future. Additionally, ample evidence suggests that these types of rivers, due to their inherent productivity, were and continue to be productive environments for salmonids and other coldwater fishes [7,13–16]. Understanding how large volcanic spring-fed rivers function ecologically and how they differ from runoff rivers is critical to the future conservation of coldwater biota. Here, we combined a literature review with over a decade of research on volcanic spring-fed rivers in Northern California, USA to understand the principal geomorphic and ecological differences between volcanic spring-fed and runoff rivers, the response of volcanic spring-fed rivers to climate change, and the implications for coldwater biota, and why these systems are critical and historically undervalued habitats for coldwater fishes.

2. Volcanic Spring Geology and Physical Processes

The global occurrence of large volcanic springs (>2.83 m^3s^{-1}) is principally a function of the geologic environment, with highly permeable extrusive volcanic rocks, such as basalts and andesite, as dominant hosts [17]. Meinzer [17] noted that more than half of the 65 large spring systems in the United States originated in the young volcanic landscapes of Idaho's Snake River basin and the Cascade Volcanic Range of Oregon and northeastern California. Geologic structures generally govern spring locations, while rock permeability and regional precipitation influences spring flow volumes. In the volcanic landscapes of western North America, groundwater typically travels through joints and fractures in volcanic rocks and through rubble zones at the contacts between lava flows [18] or along faults. Spring locations are often determined by impediments to lateral groundwater flow, such as contacts between porous volcanic rocks and less permeable sedimentary rocks [19,20]. Basaltic lava flows may also contain remnant lava tubes that provide zones of very high hydraulic conductivity, resulting in rapid aquifer recharge and groundwater transport.

In California and Oregon, most large springs are found within young (<7 million years) volcanic rocks that form the crest of the northern California and Oregon Cascades [21] or cap lower elevation areas between volcanic centers. These volcanic rocks are extremely permeable, with snowmelt and rainfall infiltrating and recharging regional groundwater. The groundwater systems developed within these young volcanic aquifers generally emerge down-gradient as anomalously large spring-fed rivers [22–24]. For instance, most large volume springs in the northern California Cascade region, including Big Springs Creek (Klamath Basin), Hat Creek, and the Fall River, are slightly thermal [25,26] and are generally thought to result from deep, regional-scale groundwater flow. Many of the smaller, coldwater springs, which create spring-fed rivers, represent shallower, local-scale groundwater flows (Figure 1). The unique characteristics of thermal and slightly thermal springs suggest that deep flow paths encounter magmatic heating [19,25–27]. Elevated chloride concentrations and excess nitrogen gas in groundwater discharged at thermal springs throughout the central and southern Cascades (see [21,26,28]) suggest these deep groundwater flow paths encounter organic-rich sedimentary rocks underlying young volcanics. Similarly, high chlo-

ride and nutrient concentrations in selected slightly thermal springs [25] suggest that these large groundwater sources may also be intercepting/interacting with organic-rich strata underlying volcanic cover [21], with important implications for ecosystem productivity.
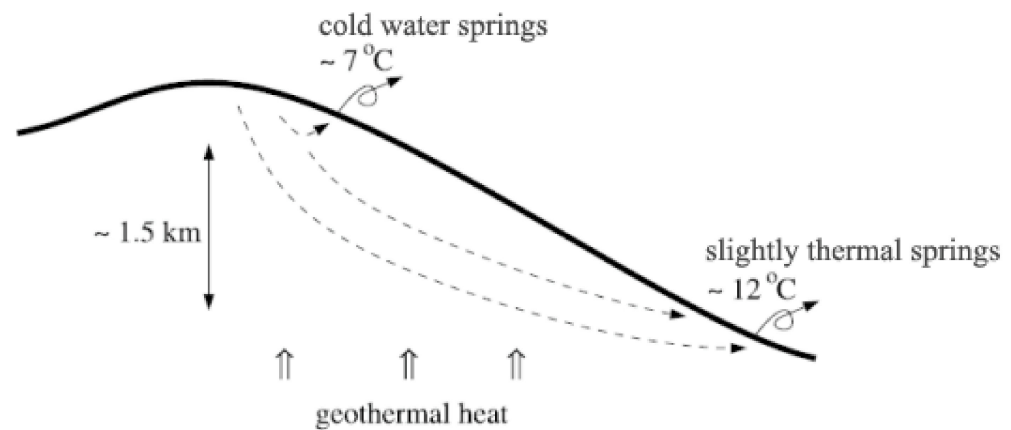
Figure 1. Conceptual diagram indicating flow path differences between shallow coldwater springs and slightly thermal springs from volcanic regions. Adapted from [29].

Biological activity in stream ecosystems is often limited by the availability of nitrogen and phosphorus, as demand for these nutrients often outweighs supply [30]. Although the magnitude of response often varies, empirical studies have demonstrated that even modest increases in a limited nutrient can directly increase primary production with cascading effects to higher trophic levels [31–33]. Elevated levels of nitrogen in stream ecosystems have most commonly been associated with anthropogenic sources (e.g., agricultural runoff, livestock, and development). Holloway et al. [34], however, showed that "geological" sources of nitrogen can contribute to elevated concentrations of nitrate in surface waters. Specifically, Holloway et al. [34] and Holloway and Dahlgren [35] identified soil nitrogen saturation through the weathering of sedimentary and metasedimentary rocks containing ecologically significant nitrogen concentrations (500–1200 mg N/kg rock). Excess soil nitrogen resulted in the leaching of nitrate to adjacent lotic ecosystems. This leaching of nitrogen from bedrock or soil can also generate elevated concentrations of nitrate in shallow and deep aquifers.

Dahlgren et al. [36] suggested that regional groundwater flow discharging at a large volcanic groundwater spring complex at the base of Mount Shasta in northern California contained nitrogen and phosphorus released from marine sedimentary and volcanic rocks encountered along the groundwater flow path. Geologic conditions that enable regional groundwater to leach nitrogen from bedrock and sediments underlying volcanic terrains may contribute to elevated nitrogen observed in groundwater springs throughout the Cascades. For example, in examining six rivers in the upper Sacramento drainage of California, Lusardi et al. [15] found that nitrate and phosphate concentrations were, on average, 40 times greater in slightly thermal volcanic spring-fed rivers than runoff rivers in the same watershed. Both Dahlgren et al. [36] and Lusardi et al. [15] also found that high nutrient concentrations associated with spring accretions strongly influenced stream ecosystem productivity.

3. Spring-Fed River Geomorphology

The geomorphic attributes of volcanic spring-fed rivers differ greatly from runoff systems. Many volcanic spring-fed rivers emerge as large rivers in topographically flat regions with poorly developed drainage networks [10,37–39]. These areas are often locations where geologic contacts (stratigraphic or structural) between rock units create permeability contrasts, forcing groundwater to the surface to form springs [10]. These flows are neither derived nor supported by overland or in-channel flows from a larger watershed. Thus,

they lack the stream power, competence, and sediment budget typical of runoff streams that have high winter or spring pulse flows. This characteristic is often reflected in their unusual and relatively static channel morphology.

The geomorphic processes associated with spring-fed rivers are largely dependent on locally derived materials and stable annual discharge [10,37]. Volcanic spring-fed rivers are often dominated by smaller substrate classes, such as sands and gravels, exhibit poorly developed channel bar features, rectangular cross-sections, and large width-to-depth ratios when compared with runoff rivers [10,37,40]. Traditional geomorphic features, such as pool/riffle sequences, are irregular and simplified [10]. These characteristics are consistent with the relatively muted hydrology exhibited by spring-fed rivers and a lack of upstream sediment supply, which also contributes to a lack of bedform complexity. Channel morphology and habitat complexity in these systems are instead dependent on the instream production of aquatic plants (e.g., rooted vascular macrophytes) and the input of large woody debris [38,39,41,42].

Roughness coefficients (Manning's n) of spring-fed rivers are comparatively large in contrast to runoff systems due to long-term retention of large wood and to macrophyte production [10,38,43]. Due to the stable nature of discharge associated with volcanic spring-fed rivers, large wood inputs are frequently retained in these systems [44]. Such wood is often orientated perpendicular to the channel, leading to increased roughness coefficients, lateral flow expansion, and increased cross-sectional area. This, in turn, can lead to the formation of vegetated islands due to flow separation [10]. Similarly, the seasonal production of aquatic macrophytes contributes to enhanced roughness coefficients associated with these systems [45]. During the growing season, aquatic macrophyte densities can be substantial [42,46], strongly affecting channel morphology and complexity, sediment transport, and biological processes.

4. Macrophytes and the Stream Environment

Aquatic macrophytes play a critical role in the ecology and physical processes associated with volcanic spring-fed ecosystems (Table 1). While their distribution is often limited in runoff systems, macrophytes are a seasonally dominant habitat feature in many volcanic spring-fed rivers. Variability in temperature, discharge, nutrients, light availability, and substrate composition have all been correlated with macrophyte distribution in fluvial systems [46–52]. Due, in large part, to their catchment topography, reliance on deep groundwater flow, and a continual influx of geologically derived nutrients, volcanic spring-fed rivers exhibit many of the abiotic factors necessary for promoting macrophyte recruitment and growth.

Table 1. Abiotic and biotic effects associated with aquatic macrophytes on volcanic spring-fed rivers.

Type of Effect	Effect	Reference
Abiotic	Reduce water velocity	[53]
	Increase stream depth	[53]
	Increase cross-sectional area and wetted habitat	[45]
	Modification of channel hydraulics	[54]
	Reduce water temperature through shading	[46]
	Enhance streambed stability	[55]
	Contribute to nutrient cycling	[56]
Biotic	Provide habitat for epiphytes, inverts. and fishes	Various
	Velocity heterogeneity and refuge for organisms	[57]
	Retain fine sediment and organic matter	[58]
	Increase prey availability for consumers	[7]
	Increase invertebrate drift rates	[7]
	Provide predator refuge	[59]
	Food resource for detritivores	[60]
	Food resource for herbivores	[61]
	Provide habitat complexity and heterogeneity	[57]
	Provide habitat cover for fish	[62]
	Increase invertebrate richness and density	[57]
	Increase fish density	[59]
	Reduce intraspecific competition in fish	[59]

The physical effects of aquatic macrophytes on spring-fed systems are extensive. Lotic macrophytes are known to reduce water velocity, increase stage and wetted surface area, modify flow patterns, retain organic matter, and aid in fine sediment deposition [41,52,58,63–65]. Champion and Tanner [45] found that macrophytes reduced water velocity by 41% and compensated for strong reductions in seasonal discharge by maintaining channel depth and cross-sectional area. Similarly, Willis et al. [46] found a strong negative relationship between plant biomass and stream water velocity, but a positive relationship between macrophyte biomass and river stage in Big Springs Creek in northern California. The strong seasonal pattern of macrophyte growth and residual effects on the physical environment has important implications for stream biota and may be particularly important during key parts of the annual hydrograph, during dry water years, or when water demands may be in conflict.

Shifts in the availability of wetted habitat may also be accompanied by changes in channel hydraulics due to the growth and annual senescence of aquatic macrophytes. Cotton et al. [41] found that the seasonal growth of macrophytes formed alternating channels of erosional and depositional environments. Nepf [52] showed that dense areas of submerged and emergent aquatic vegetation affect stream hydraulics on the reach scale, which influence ecological processes like nutrient uptake, deposition, and channel stability on a comparable scale. Similarly, Willis et al. [46] found that the seasonal growth of macrophytes in Big Springs Creek drastically shifted channel hydraulics, providing velocity heterogeneity and habitat complexity for stream biota (Figure 2). Preceding substantial macrophyte growth during spring, channel velocities appeared homogenous, as flow was primarily routed through high-velocity channels. However, continued macrophyte growth reduced water velocity and caused a shift in hydraulic diversity (Figure 2). This seasonal evolution of channel hydraulics provides a mosaic of habitat conditions conducive to juvenile salmonid rearing. Low-velocity channels likely provide predator and velocity refuge, and access to higher velocity drift feeding stations [7]. These sites are also natural areas for organic matter deposition [58], important resources for foraging macroinvertebrates and fishes. Conversely, high-velocity channels serve as migration/movement corridors, scour fine sediments, and expose gravel habitat for spawning adults.
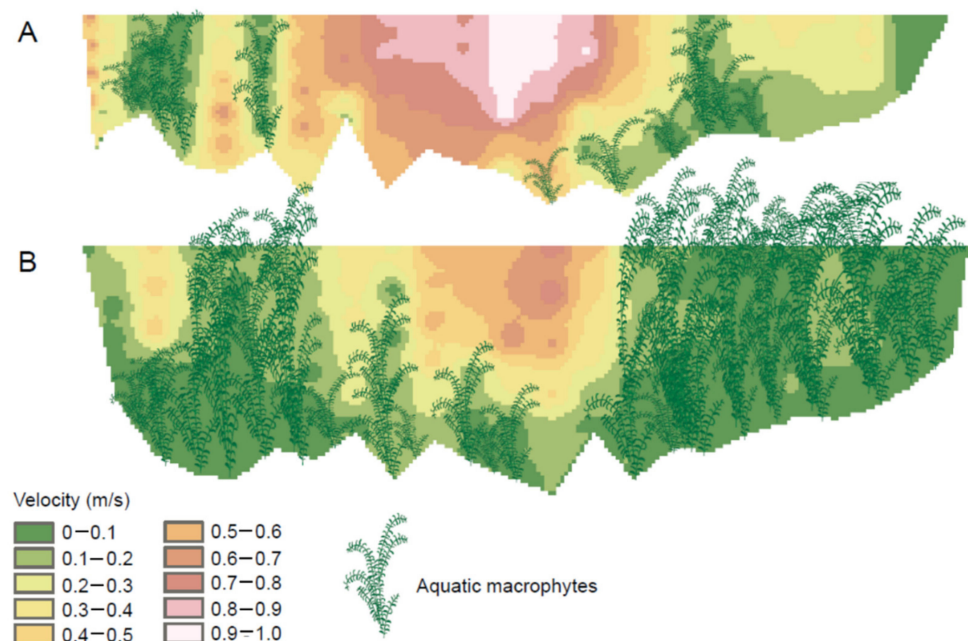
Figure 2. Seasonal evolution of channel hydraulics and velocity heterogeneity in a volcanic spring-fed river in northern California. Increasing plant biomass between seasons reduces high-velocity channels and provides velocity heterogeneity for biota. Seasonal minimum macrophyte biomass (93.5 g/m^2 Ash Free Dry Mass; March 2011) (**A**) and maximum macrophyte biomass (390.9g/m^2 Ash Free Dry Mass; August 2011) (**B**). (Adapted from [46]).

Unlike the relationship between macrophytes and stream hydraulics, less has been published about the effect of macrophytes on stream temperature. Until recently, studies explored this relationship at the patch scale and revealed an intuitive relationship between the slower hydraulics of water moving through macrophytes and warmer stream temperatures in the surface flow layer [66]. When studied at the reach scale, however, macrophytes become a seasonal control of spring-fed thermal regimes at both the local and reach scales. Extensive emergent macrophyte growth forms a seasonal riverine canopy and creates a buffer against warming [46,67]. Within reaches where extensive, emergent macrophyte growth occurs, spring-fed streams reach their annual maximum temperatures over 30 days earlier than runoff streams and have less diurnal heating during what is typically the warmest period of the year [46]. These effects can be exported for tens of kilometers downstream from voluminous spring sources, creating unique and predictable thermal patterns and improving water quality for coldwater habitats [42,68].

Macrophytes also exert an appreciable effect on nutrient cycling. Most are capable of acquiring nutrients from both streambed sediments through their roots [69] and directly from the water column via their leaves, substantially shifting stream water nutrient dynamics [70]. Mount et al. [43] showed that longitudinal seasonal declines in nitrate concentrations from source springs were strongly correlated with seasonal shifts in macrophyte biomass, while Riis et al. [56] showed that macrophytes increased nutrient uptake rates, lowered turnover rates, and reduced downstream nutrient exports.

5. Macroinvertebrate Communities

The influence of abiotic and biotic factors in structuring stream macroinvertebrate communities has received ample attention in the ecological literature [56,71–73]. While each is capable of influencing lotic macroinvertebrate communities, the relative strength of biotic interactions such as predation, competition, and facilitation may ultimately be determined by local environmental conditions and, at broader spatiotemporal scales, biogeographic history. In terms of the abiotic environment, volcanic spring-fed rivers vary greatly from runoff systems. For instance, while both the flow and thermal regime of spring-fed systems can be described as stable, the opposite is true for runoff systems, and this has important implications for macroinvertebrate community dynamics, life-history traits, reproductive cues, and growth rates [15].

Spring-fed river macroinvertebrate communities differ significantly from runoff systems in numerous ways. In comparing multiple small volcanic spring creeks and runoff systems in the Cascades, Yamamuro [74] found that semi-voltinism, emergence asynchrony, and slow growth rates were strong indicators of spring-fed macroinvertebrate communities, whereas macroinvertebrates associated with runoff systems exhibited additional life-history strategies. These differences were attributed to variations in flow regimes between river types. Strong selection pressure associated with flow variability in runoff systems likely caused macroinvertebrate communities to favor rapid development time and earlier reproduction in order to avoid high flow mortality-inducing events. Life history and behavioral adaptations of macroinvertebrates to flow regimes may be prompted by a combination of strong selection pressure and predictability of disturbance events [75–77].

Differences in temperature may also play an important role in macroinvertebrate community dynamics between river types. In a reciprocal transplant study, Yamamuro [74] showed that a common stonefly, *Yoraperla nigrisoma*, inhabiting paired spring-fed and runoff rivers developed more rapidly when transplanted from its native spring-fed habitat to a runoff stream. The author concluded that changes in development time were associated with greater abiotic variability in runoff systems and, more specifically, elevated water temperature during the study period. While those in spring-fed systems had slower development and attained larger final body size, those in runoff streams exhibited more rapid development and smaller body size at emergence. The study demonstrated that some macroinvertebrate life-history traits are strongly dependent on the environment and that trait expression can be plastic.

Many studies suggest that spring-fed rivers are capable of supporting higher densities of aquatic macroinvertebrates than other stream types (snowmelt, rain-fed, glacial, etc.), although the mechanisms behind these findings are unclear. In two alpine streams, Füreder et al. [78] found that the density of macroinvertebrates was nearly 2-fold greater in a spring-fed river than an adjacent glacier-fed stream and attributed this disparity to environmental differences between river types. Yamamuro [74] suggested that greater macroinvertebrate densities in volcanic spring-fed creeks were directly related to differences in flow regime between river types, and Barquin and Death [79] found that macroinvertebrate abundance differences were associated with streambed stability and enhanced food resource availability in spring-fed rivers. Barquin and Death [80] found that spring-fed rivers supported higher levels of primary production and organic matter retention. The authors suggested that the flow stability of spring-fed systems reduced the downstream displacement of these resources and macroinvertebrates themselves, ultimately contributing to enhanced macroinvertebrate densities in spring-fed systems. Finally, in examining several large volcanic spring-fed rivers in the Pacific Northwest, Lusardi et al. [15] found that volcanic spring-fed rivers exhibited up to a 16-fold increase in macroinvertebrate density when compared with adjacent runoff rivers (Figure 3) in the same basin.
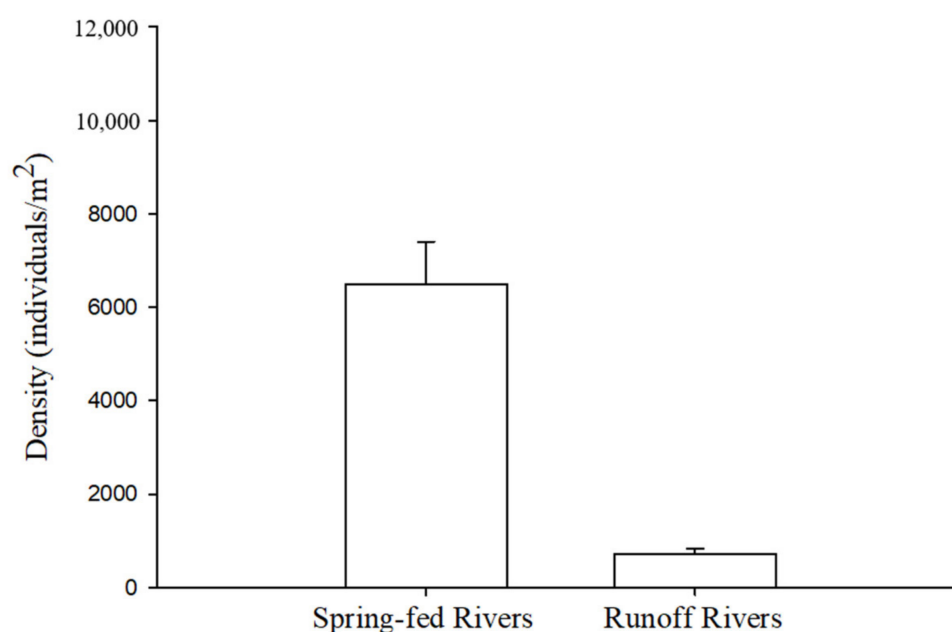
Figure 3. Comparison of invertebrate densities between three volcanic spring-fed rivers and three runoff rivers in northern California, USA. (Adapted from [15]).

Nutrient additions to stream food webs can stimulate primary production, and, in turn, enhance secondary production via bottom-up processes [32,80,81]. Nutrient availability is often greater in volcanic spring-fed rivers than runoff systems due to groundwater sources of typically limited nutrients, such as nitrogen (N) and phosphorus (P), from the underlying geology to the surface water (see [34]). These geologically derived nutrients stimulate primary productivity and indirectly affect macroinvertebrate consumer populations by increasing resource availability, and ultimately, enhancing macroinvertebrate carrying capacity [82–84].

Elevated nutrient availability may also increase habitat complexity with cascading effects to primary consumers. Using a manipulative experiment, Lusardi et al. [7] found that macrophytes increased macroinvertebrate densities by 9-fold and drift rates by nearly 3-fold when compared with adjacent gravel habitats. Similarly, Brusven et al. [85] found that stream macroinvertebrate densities were 4 to 18-fold greater in bryophyte patches when compared with typical stream bedforms, such as gravels and cobbles; others have come to similar

conclusions [86]. Such habitat-mediated effects are important contributors to differences in macroinvertebrate densities between spring-fed and runoff stream ecosystems.

6. Macroinvertebrate Diversity

While volcanic spring-fed rivers are capable of supporting high densities of macroinvertebrates, they often exhibit lower species diversity than runoff systems [15,74]. This characteristic is somewhat counterintuitive because previous studies have shown that higher macroinvertebrate abundances are positively associated with species richness [87]. Explanations vary and include both density-dependent and density-independent processes. For example, Barquin and Death [80] suggested that higher densities of macroinvertebrates intensified biotic interactions in spring-fed systems, making both predation and competition important structuring forces. Their reasoning was largely influenced by the harsh–benign hypothesis originally postulated by Menge [88] and later supported by Peckarsky [89] in lotic ecosystems. Peckarsky [89] demonstrated that predation intensity was mediated through changes in the hydraulic environment, showing a negative correlation between hydraulic turbulence and predation rate. This suggests that biotic interactions in spring-fed rivers may be more important in structuring species diversity due to the relatively benign and stable nature of the flow regime. Barquin and Death [80], however, offered additional hypotheses concerning lower richness values between river types, which were mostly aligned with density-independent mechanisms. Specifically, they argued that spring-fed systems are naturally dispersal-limited due to an absence of higher-order upstream reaches found in runoff rivers. Additionally, the authors suggested that thermal constancy associated with spring-fed systems may eliminate certain macroinvertebrate genera dependent on thermal life history cues.

Nevertheless, mechanisms controlling species richness in streams are likely to be strongly density-independent. Environmental heterogeneity may play a prominent role in structuring species diversity in spring-fed systems. One principal hypothesis, following [90], is that intermediate levels of disturbance maximize the ability of colonizers and competitors to coexist in a non-equilibrium state of high species diversity. In the absence of disturbance, a few superior competitors tend to dominate, and diversity is subsequently low as the community approaches equilibrium. Conversely, if the occurrence of disturbance is high, only effective colonizers with strong dispersal capabilities can persist, rendering community dynamics to a constant non-equilibrium state of low diversity [91]. This hypothesis suggests that low environmental heterogeneity associated with spring-fed systems may play an important role in reducing species diversity compared to runoff systems [15].

Most of the ecological literature pertaining to spring-fed systems suggests that the flow and temperature regime, and, more generally, habitat, may contribute to low macroinvertebrate species diversity. Minshall [92] proposed that flow and thermal homogeneity of spring-fed systems strongly limited available niche space, favoring the competitive dominance of a few genera. Similarly, Laperriere [93] suggested that low species diversity associated with a spring-fed system in Alaska was directly related to reductions in flow and temperature heterogeneity and used the intermediate disturbance hypothesis to explain the diversity trend. In examining 54 stream sites, Townsend et al. [94] found strong support for the intermediate disturbance hypothesis and showed that species diversity between sites was largely a function of variation in the frequency and magnitude of the particular flow regime. More recently, Barquin and Death [95] found a correlation between temperature heterogeneity and species diversity in studying nine spring-fed streams in New Zealand. Specifically, the authors found a positive relationship between temperature amplitude and taxon richness, although several potential covariates were not examined. Other authors have suggested that spring-fed systems lack seasonal habitat heterogeneity when compared with runoff systems, contributing to reductions in species diversity [74].

The dynamic equilibrium hypothesis [96] identifies the interplay between population growth rate and disturbance as the most important factor influencing diversity and may also explain assemblage patterns associated with spring-fed rivers. While the hypothesis

reflects an understanding of the effects of environmental heterogeneity on species diversity, it does not implicate specific abiotic controls on diversity. Rather, Huston [96] argues that the relative importance of biotic interactions is controlled by any factor influencing population growth rates. Runoff systems, which typically experience high flow disturbance events during the spring, more closely reflect non-equilibrium conditions due to annual population reductions associated with high flow events. Biotic interactions presumably become increasingly more important through time, as these systems shift from a non-equilibrium state immediately following a high flow event towards equilibrium conditions during the relatively stable summer and fall baseflow periods. Alternatively, in spring-fed systems, the rate of population growth is comparatively constant due to weak environmental selection pressure. These systems naturally approach competitive equilibrium, likely rendering competitive interactions more important in regulating species diversity.

Ecological theory is fraught with inherent conditionality [97]. Due, in part, to the complexity of nature and shifting conditions through space and time, few, if any, concepts can holistically and accurately predict biotic responses to variations in environmental heterogeneity. Ultimately, however, it appears that macroinvertebrate diversity patterns in spring-fed rivers versus runoff systems reflect an important tradeoff between colonization and competition dynamics, as mediated by the abiotic environment. While runoff systems are in a non-equilibrium state where diversity trends are largely dictated by abiotic conditions, spring-fed rivers are often maintained at near-equilibrium conditions due to temporal environmental stability. In turn, these conditions render biotic interactions as the primary determinant of local assemblage patterns [91,98].

7. Salmonids and Spring-Fed Rivers

Historical evidence suggests that volcanic spring-fed rivers supported robust salmonid populations in which individuals may attain higher growth rates when compared with typical runoff systems. For instance, despite accounting for less than 2% of the total annual discharge of the Lower Klamath River, the Shasta River historically produced greater than 50% of the entire Klamath fall Chinook (*Oncorhynchus tshawytscha*) run in northern California [13,14]. Rapid growth rates and early sexual maturation of Chinook parr have been documented on the Shasta River and other spring-fed rivers, a departure from typical Chinook life-history strategies [99–101]. By directly comparing the growth and age of sexual maturity in Chinook salmon between a volcanic spring-fed and runoff river in New Zealand, Unwin et al. [102] found that juvenile Chinook from the spring-fed river grew at more rapid rates and were twice as likely to mature by age two than those from the runoff river, irrespective of spawning date. In another study, Lovtang [103] showed that juvenile Chinook salmon inhabiting the headwater reaches of the volcanic spring-fed Metolius River exhibited superior growth rates when compared with four other tributaries within the basin. Numerous factors, including both environmental and genetic, likely contributed to these findings.

Runoff systems show high variability in their thermal and flow regimes (Figures 4 and 5). These two abiotic factors induce significant selection pressure on salmonid populations. Davidson et al. [104] found that discharge and temperature were the most important factors affecting salmonid growth rates during their first year of survival and others have shown that these variables can strongly limit the distribution and growth of juvenile salmonids [105,106]. In particular, peak flow episodes can initiate mortality events through displacement [107], stranding [108], bed scour [109], and energetic costs of individuals, while low flow events can lead to population bottlenecks through reductions in available wetted habitats or an increase in water temperature (e.g., [110]). Similarly, seasonal water temperature fluctuations in runoff rivers can greatly affect coldwater fishes by increasing physiological stress, metabolic demand, and the probability of disease proliferation during summer and fall, and by reducing body condition and energy reserves during winter [111].
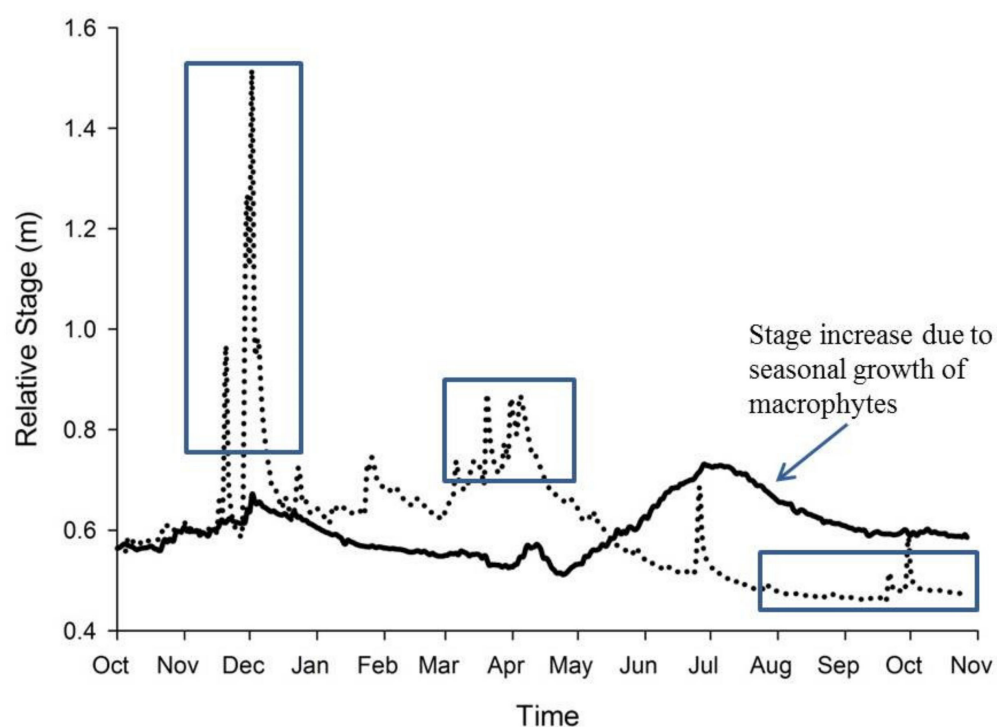
Figure 4. Comparison of stage fluctuations on a volcanic spring-fed river (solid line) and a runoff river (dotted line) in northern California, USA. Rectangles indicate typically stressful periods for fish with high discharge events occurring during the winter and spring, and low flow periods during the late summer and fall. (Adapted from [15]).
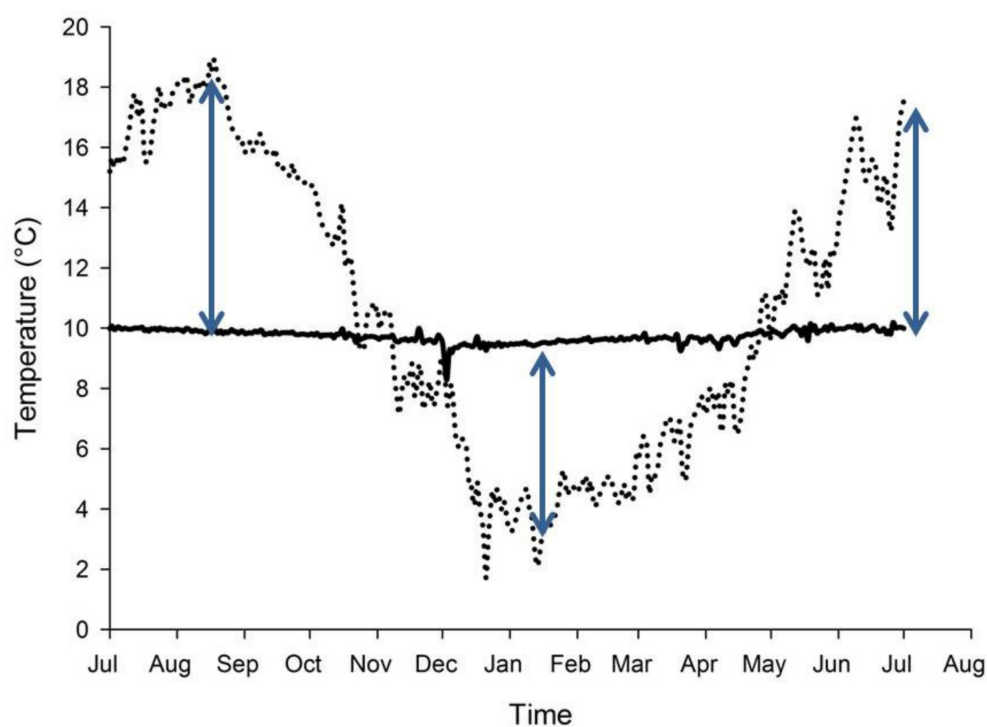
Figure 5. Comparison of thermal fluctuations on a volcanic spring-fed river (solid line) and runoff river (dotted line) in northern California, USA. Arrows indicate typically stressful periods for fish and other coldwater biota. (Adapted from [15]).

In contrast, volcanic spring-fed rivers typically show annual flow and thermal constancy (Figures 4 and 5). Ecologically, this has important implications for stream biota. First, available wetted habitats remain relatively stable throughout the year (Figure 4). This may be especially important for fall spawning salmonids when available habitats may otherwise be limited (as such in runoff rivers), thus providing a catalyst for density-dependent mortality (see [112]) or during over-winter periods, which has been shown to affect smolt production [113]. Secondly, the elimination of high flow events strongly reduces the potential for environmentally stochastic events to negatively affect salmonid population dynamics (see Figure 4). In a runoff stream, Jensen and Johnsen [114] found a strong positive correlation between the magnitude of the spring peak flow and juvenile salmonid mortality and that growth rates were reduced in years with higher peak flows. Others have found that high magnitude and sporadic flow events immediately following spawning can greatly reduce salmonid recruitment rates [115,116]. Indeed, flow stability, and more generally, stable environmental conditions may be an important factor influencing the resident salmonid selection of tributaries. Koizumi and Maekawa [117] found that one of the strongest predictors of Dolly Varden (*Salvelinus malma*) presence was their strong preference for spring-fed creeks and attributed this finding to the constancy of the flow regime.

Water temperature, and more generally, thermal habitat, has also been shown to be a limiting factor in the distribution of salmonids during over-summer and winter periods in runoff systems [118,119]. Extreme temperature fluctuations can induce mortality, negatively affect growth rates, and have non-lethal ontogenetic effects [120,121]. In stark contrast to runoff rivers, spring-fed systems exhibit stable thermal patterns throughout the year and this has important implications for the growth and survival of salmonids (Figure 5). In studying the overwintering survival of rainbow trout at different locations along the Snake River, Idaho, Smith and Griffith [122] noted that while up to 43% of individuals experienced winter mortality at non-spring sites, all individuals residing near spring sources survived. Olsen and Young [123] found that the growth potential of brown trout was greatest near a volcanic spring source because water temperatures were substantially lower and created thermal refuge from elevated mainstem conditions. The use of volcanic springs as thermal refuges for rearing salmonids was further documented on the Shasta River in northern California, where juvenile coho were shown to migrate up to 6 km to access upstream spring habitats during summer [124]. Null and Lund [125] posited that complete restoration of coldwater habitats in this system could increase coho smolt production by 542%.

Other factors also likely play an important role in the growth of salmonids in volcanic spring-fed rivers. Due to relatively large nutrient input from geological sources in some systems, particularly inorganic nitrogen and phosphorus, the food web of these systems may be principally controlled by bottom-up processes. Numerous empirical studies demonstrate that even modest increases in a limiting nutrient can directly increase primary production with cascading effects to higher trophic levels (e.g., [81], and a few studies have found that nutrient additions can increase the growth of juvenile salmonids via bottom-up processes [32,126]. This suggests that nutrient-rich waters, such as volcanic spring-fed rivers, are inherently capable of supporting enhanced salmonid growth rates due to the appreciable quantities of typically limited nutrients that naturally occur in these systems. Augmented growth rates seem especially probable in consideration of the aggregate effects of temperature, discharge, and trophic dynamics on salmonid growth in volcanic spring-fed rivers.

Habitat may also be an important consideration for the growth of salmonids in volcanic spring-fed rivers. Much of the literature concerning the use of traditional forms (pools, large wood, etc.) of salmonid habitats has focused on the interplay between energy expenditure and food availability, often reflecting on optimal foraging theory [127–129]. Critical to the understanding of favorable salmonid habitat is the relative role and relationship between prey availability, stream velocity refuge, structural complexity, and competition

between individuals for dominant positions (or the specific carrying capacity of a habitat unit or reach of stream influencing competitive hierarchies), among other factors. Habitat selection, and, more generally, the growth and survival of stream-rearing salmonids, is often determined by the interaction among these variables with more dominant individuals often occupying habitats that maximize these factors. In runoff streams, pool habitats and large wood have received extensive consideration as superior salmonid habitats because of the interaction and balance between the aforementioned factors that influence growth and survival [130–134].

In contrast, as previously discussed, macrophytes constitute a dominant habitat feature in many volcanic spring-fed systems [42,46,68]. While lotic macrophytes have rarely been studied as salmonid habitats (see [7,62]), many of the same mechanisms that benefit the growth and survival of salmonids in runoff systems are also apparent with non-traditional forms of habitat, such as aquatic macrophytes. Lusardi et al. [7] found that juvenile steelhead (*Oncorhynchus mykiss*) overwhelmingly preferred macrophyte habitats when compared with five alternative habitat types on a large spring-fed river in northern California, and found that macrophyte habitats reduced water velocity and improved prey availability and drift for foraging fish. Riley et al. [135] noted that salmonid size was positively correlated with macrophyte cover and suggested that this type of habitat provided salmonids with velocity refuge and access to significant food resources. Similarly, Beland et al. [62] found that juvenile Atlantic salmon preferred intermediate densities of macrophyte habitats because they reduced water velocity, provided cover from predators, and increased prey availability. Heggenes et al. [136] found that submersed vegetation was an important over-wintering habitat for brown trout, and others have come to similar conclusions [137].

There are additional benefits to salmonids associated with macrophyte habitats. Structurally complex habitats in rivers, such as large wood, have been shown to increase the carrying capacity of stream-rearing salmonids and reduce intraspecific competition [133–138]. While the mechanisms behind these findings are not entirely clear, habitat complexity provides an important balance between resource availability, predator and velocity refuge, and visual isolation from conspecifics [139]. This latter effect has been deemed important in reducing physiological stress from aggressive interactions associated with dominance hierarchies, which can reduce growth rates and induce mortality [140]. Similar to more traditional forms of salmonid habitat, aquatic macrophytes may also provide similar benefits to salmonids. In a manipulative study, Eklov and Greenberg [59] found that the addition of artificial macrophytes to a stream significantly increased the density of juvenile salmonids when compared with barren reaches. The authors attributed their results to both increased refuge from terrestrial predators and visual isolation from congeners. We suggest that aquatic macrophytes confer benefits similar to more traditional salmonid habitat forms and positively affect salmonids in numerous ways [7,141] (Figure 6).

Cumulatively, the effects of habitat, environmental stability, and food web dynamics on higher-order consumers, such as salmonids, have broader conservation and recovery implications. Unique rearing habitats, which substantially improve the growth and body condition of juvenile salmonids, relative to other habitats, have been shown to significantly influence adult return success from the marine environment [142]. Beakes et al. [143] found a strong positive correlation between smolt size at ocean entry and adult return, suggesting that ocean phase mortality was size-dependent. Additionally, because volcanic spring-fed rivers are numerically rare compared with their runoff counterparts, they offer a high intrinsic potential for the recovery of imperiled species due to their implicit contributions to landscape habitat heterogeneity, which may contribute to a diversity of life-history strategies, including differences in outmigration timing and the size of juveniles. For instance, Chinook salmon have been shown to sexually mature as parr and participate early in spawning in spring-fed rivers but not elsewhere [99–101]. This may be a reproductive adaptation to bet-hedge against the potential for high mortality

events associated with episodic poor marine conditions. Under such circumstances, this reproductive strategy may reduce overall population complex losses during certain years via a portfolio effect [144]. Others have found that salmonids experience enhanced growth rates and earlier emergence in spring-fed rivers compared with runoff systems [102,103]. Diversity in life-history timing and, more generally, growth, may allow for earlier ocean migration timing or provide a size-selective advantage to particular individuals within a population complex. Such advantages may, for instance, dampen the effects of an early marine upwelling event or a size-dependent mortality event (i.e., predation) to a larger salmonid population complex. Ultimately, the environmental heterogeneity associated with spring-fed rivers plays an integral role in fostering interpopulation diversity within salmonid populations and may be an undervalued contributor to stock resiliency.
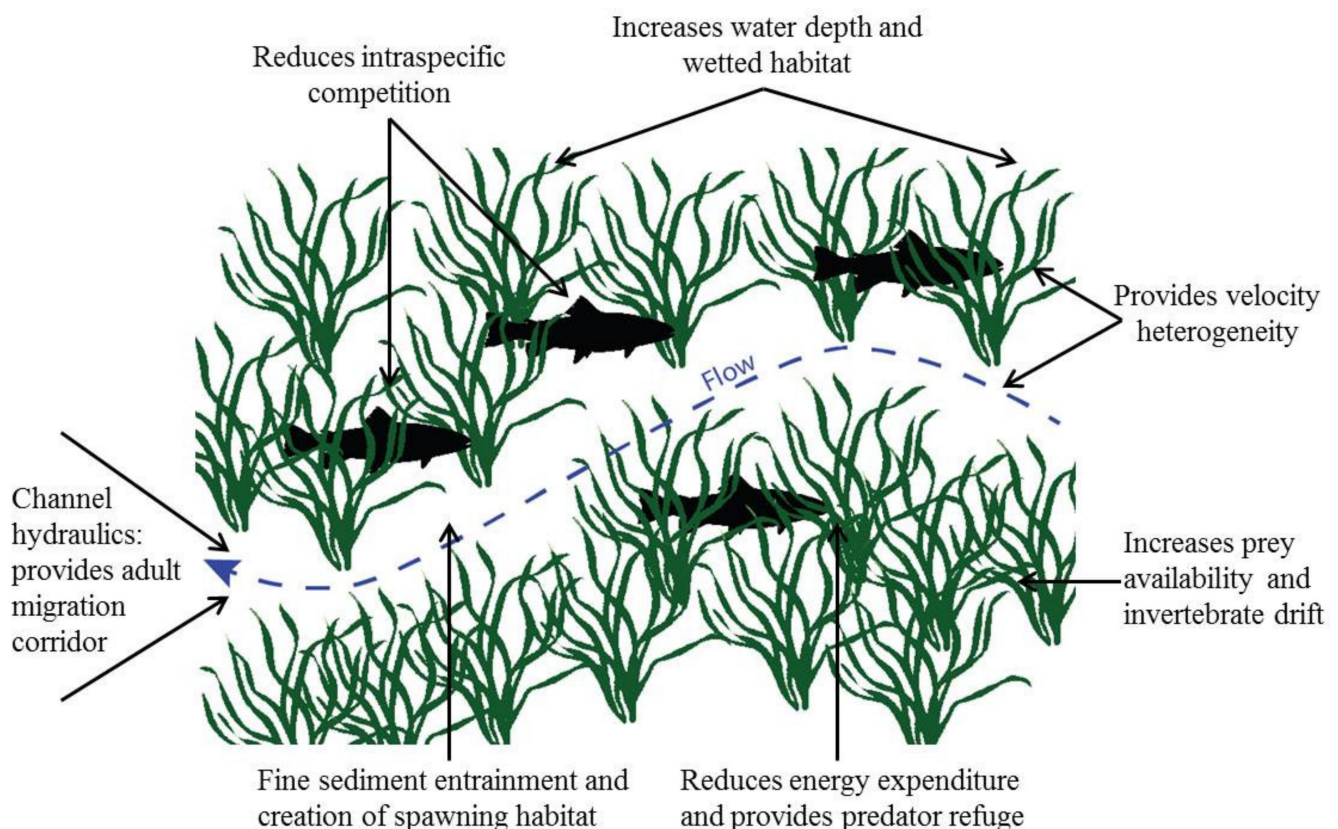
Figure 6. Conceptual model displaying multiple positive species effects of aquatic macrophytes on salmonids in volcanic spring-fed rivers.

8. Spring-fed Rivers and Climate Change

Coldwater species, such as Pacific salmonids, are expected to be increasingly exposed to deteriorating habitat conditions with the advancement of climate change. Some models suggest that by 2100, more than 60–90% of all coldwater habitats will become marginalized [145]. Others project nearly a 50% decline in habitats for all trout species by 2080 [4]. These projections are primarily driven by rising air temperatures and a declining snowpack. For instance, Hayhoe et al. [146] suggest that the Sierra Nevada may experience a 30–90% reduction in snowpack by 2100, depending on emission scenarios. Specifically, coldwater habitat decline will likely be manifested through an earlier spring runoff period and concomitant extension of the summer and fall baseflow period, higher magnitude peak flows during the winter, and, more generally, broad annual reductions in streamflow [24,147,148]. Some have implicated these shifts in the abiotic environment to favor alien species, and, in turn, negatively affect native coldwater species through biotic interactions [4,149]. Not

surprisingly, Moyle et al. [3] recently found that 87% of all California native salmonids were either critically or highly vulnerable to climate change.

Recently, some authors have suggested that the geologic landscape or context of a particular basin should be taken into consideration when predicting the effects of climate change on coldwater habitats, rather than generalized models [23,150–152]. Spring-fed systems are groundwater-dependent and often form in geologic areas dominated by young volcanic rocks, such as basalt and andesite, which have high conductivity and storage capacity. These volcanic terrains, prevalent in the Pacific Northwest Cascade region, often have deep groundwater aquifers that feed many spring-fed systems. In turn, this profoundly affects the hydrology of these systems, with stream discharge often lagging behind actual runoff events due to drainage characteristics [24,153].

Tague et al. [154] and Tague and Grant [150] demonstrated that volcanic spring-fed systems have the ability to dampen the effects of climate change because of their ability to store water with the onset of snowmelt and infiltration. Due to a groundwater storage effect and time lag between precipitation and streamflow associated with young volcanic landscapes, spring-fed systems are the beneficiaries of sustained baseflow periods and persistent coldwater habitats. Conversely, with the onset of climate change, snowmelt will run off earlier and the proportion of precipitation as rain will increase, thus extending low baseflow periods and leading to temperatures exceeding the physiological optima of coldwater species in runoff-dominated rivers. The phenomenon may be exacerbated by increasing water demand for agricultural and other consumptive purposes [155].

Alternatively, in spring-fed systems, elevated baseflow marked by cooler water temperatures are likely to be sustained due to groundwater storage and residence time effects. This suggests that volcanic spring-fed systems, due to their distinctive geology and hydrology, may be future strongholds for coldwater species such as salmonids. Tague et al. [154] cautioned, however, that volcanic spring-fed systems will likely experience overall larger absolute declines in streamflow than snowmelt systems because they typically contain greater volumes of water, and their source of water (snowpack) is also in decline. However, Howat et al. [156] demonstrated that glaciers associated with Mt. Shasta in the southern Cascade Range have grown during the 20th century due to increasing precipitation negating the effects of increasing air temperature. This suggests that in some cases, volcanic spring-fed rivers (particularly those in the Shasta Valley of northern California) are uniquely positioned to be coldwater refuges for the foreseeable future.

In addition to dampening the effects of shifts in temperature and discharge on coldwater species, fish in volcanic spring-fed rivers may also be resilient to climate change for other reasons. The growth of stream salmonids is controlled by the balance of energy intake (resource consumption) and loss (respiration, egestion, and excretion) [157]. As stream temperature increases above the physiological optima, salmonid respiration and metabolic demand also increase. If the increase in metabolic demand is not balanced by consumption, a net deficit will lead to declining growth. However, incremental increases in metabolic demand may, to some extent, be compensated for by increases in prey consumption. For instance, Lusardi et al. [16] found that growth rates of juvenile coho improved under warming water conditions where sufficient food existed in a volcanic spring-fed river in northern California. This suggests that more productive habitats may be more resilient to warming stream temperatures with the onset of climate change [15,16]. As previously discussed, volcanic spring-fed rivers exhibit high productivity and support robust populations of macroinvertebrate prey for salmonids, especially when compared with runoff rivers. Due to their unique hydrology and biotic conditions, volcanic spring-fed rivers are well-suited to be coldwater refuges under a warming climate.

9. Conclusions

Much of our knowledge on lotic ecosystem form and function is based on the extensive scientific literature regarding runoff rivers. While traditional stream ecology theories, such as the River Continuum Concept [158] or Flood Pulse Concept [159], provide a solid

conceptual framework to understand riverine processes, these theories have little relevance to volcanic spring-fed systems. Volcanic spring-fed rivers, therefore, require an integrated understanding of the abiotic and biotic processes driving ecosystem function [12].

While volcanic spring-fed rivers are relatively rare compared to runoff rivers, they offer substantial benefits for the conservation of coldwater species, particularly salmonids. Rarely studied salmonid habitat forms, such as aquatic macrophytes, play an integral role in both the physical and ecological processes of volcanic spring-fed rivers and positively affect salmonids in numerous ways. The mechanisms contributing to profitable stream positions for salmonids remain largely intact with macrophyte habitats but appear in non-traditional forms. The stable nature of these ecosystems generally results in a less diverse macroinvertebrate community when compared with runoff rivers. However, when coupled with geologically derived nutrients, such as nitrogen and phosphorus, these systems exhibit exceedingly high standing crops of aquatic macroinvertebrates, important prey resources for salmonids.

Finally, climate projections suggest radical shifts in stream discharge and temperature regimes throughout the western United States and elsewhere, and these changes are expected to further imperil coldwater species such as salmonids. Resource managers will become increasingly reliant on volcanic spring-fed rivers as these climate-induced changes continue to marginalize coldwater habitats. While we believe that stable discharge and temperature regimes of these spring-fed systems make them resilient to a changing climate, we are also confident that high levels of ecosystem productivity provide additional insurance to coldwater species.

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