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Legacy effects of wildfire on stream thermal regimes and rainbow trout ecology: an integrated analysis of observation and individual-based models

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Abstract: Management of aquatic resources in fire-prone areas requires understanding of fish species' responses to wildfire and of the intermediate- and long-term consequences of these disturbances. We examined Rainbow Trout populations in 9 headwater streams 10 y after a major wildfire: 3 with no history of severe wildfire in the watershed (unburned), 3 in severely burned watersheds (burned), and 3 in severely burned watersheds subjected to immediate events that scoured the stream channel and eliminated streamside vegetation (burned and reorganized). Results of a previous study of this system suggested the primary lasting effects of this wildfire history on headwater stream habitat were differences in canopy cover and solar radiation, which led to higher summer stream temperatures. Nevertheless, trout were present throughout streams in burned watersheds. Older age classes were least abundant in streams draining watersheds with a burned and reorganized history, and individuals >1 y old were most abundant in streams draining watersheds with an unburned history. Burned history corresponded with fast growth, low lipid content, and early maturity of Rainbow Trout. We used an individual-based model of Rainbow Trout growth and demographic patterns to determine if temperature interactions with bioenergetics and competition among individuals could lead to observed phenotypic and ecological differences among populations in the absence of other plausible mechanisms. Modeling suggested that moderate warming associated with wildfire and channel disturbance history leads to faster individual growth, which exacerbates competition for limited food, leading to decreases in population densities. The inferred mechanisms from this modeling exercise suggest the transferability of ecological patterns to a variety of temperature-warming scenarios.

Key words: Rainbow Trout, wildfire, temperature, life history, disturbance

Disturbance, such as wildfire, is a fundamental component of ecosystems (Sousa 1984). In riverine ecosystems, disturbance often is manifested through floods and droughts, which have immediate effects but also may create intermediate- to long-term changes in habitat configurations that can shape aquatic species' life history, behavior, and morphology (Lytle and Poff 2003, Stanley et al. 2010). Thus, as the nature, pattern, and history of disturbance change over time and space, so too may the characteristics

of the species and ecosystems themselves (Parmesan 2006, Hof et al. 2008, Reed et al. 2011). In particular, change in stream disturbance regimes is a likely prospect if future climates warm (Wenger et al. 2011, Arismendi et al. 2012), especially if warming leads to increased incidence and severity of wildfire (Westerling et al. 2006, Rieman et al. 2010). Within the course of hours to days, wildfires can burn forests and riparian vegetation in headwater stream watersheds, and the combination of severe wildfire and pre-

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precipitation soon after disturbance can trigger landslides, debris flows, and floods that can scour the stream channel to bedrock (Benda et al. 2003, Miller et al. 2003), leading to immediate mortality of fish and uprooting and removal of riparian vegetation (Bozek and Young 1994, Rieman et al. 1997, Brown et al. 2001). Loss of canopy cover and riparian vegetation and the consequent warming of stream temperatures can persist for decades (Dunham et al. 2007, Isaak et al. 2010, Mahlum et al. 2011).

Loss of terrestrial vegetation and geomorphological disturbance after wildfire may cause immediate local extirpation of fish, but they may recover quickly to predisturbance abundances or distributions (Dunham et al. 2007, Sestrich et al. 2011). Studies of streams with a history of wildfire in their watersheds suggest that fish movement and habitat connectivity play an important role in this rapid recovery (Rieman et al. 1997, Neville et al. 2009), but phenotypic changes in individual fish in response to altered environmental conditions, most notably temperature, also may contribute to apparent resilience (Kammerer and Heppell 2012, McMillan et al. 2012). We investigated this possibility in an analysis of age-specific population density, growth, condition, and development of Rainbow Trout (*Oncorhynchus mykiss*) in streams with different thermal regimes resulting from a history of stand-replacing wildfires and channel-reorganizing events (Dunham et al. 2007, Rosenberger et al. 2011).

We compared the ecology of Rainbow Trout in streams in watersheds representing 3 different wildfire histories, from those without stand-replacing wildfire in the last century (unburned) to those that experienced severe wildfire ~10 y before to our study (burned) to those that experienced both wildfire and subsequent stream channel reorganization from postfire flooding and debris flows ~10 y before our study (burned and reorganized). This history has been linked to lasting differences in canopy cover and stream temperatures. The warmest temperatures are associated with loss of both coniferous upland vegetation and deciduous riparian vegetation (Dunham et al. 2007, Isaak et al. 2010). We sampled fish from 9 streams (3 in each disturbance history category) and compared population density, size at age, condition, and development (gonadal maturation) of individuals to provide an empirical evaluation of fish responses to these contrasting environments. We developed and applied an individual-based model to simulate bioenergetic and demographic responses of fish linked to temperature, food, and body size to evaluate the potential influence of changes in water temperature on resident trout. We used model results to evaluate relative differences in fish growth, size, and densities among contrasting thermal regimes, considering only the bioenergetic and competitive consequences of wildfire-associated warming. Collectively, these results allowed us to evaluate physiological, life-history, and demographic responses of Rainbow Trout to thermal regimes associated with the legacy of wild-

fire and channel reorganization. In the broader view, we interpret these findings in light of the full suite of processes that can contribute to the resilience of species, such as Rainbow Trout, to wildfire-related disturbance and habitat alteration.

METHODS

Study area and sampling frame

We studied headwater streams of the Boise River in summer 2003 and autumn 2004 (Boise National Forest, central Idaho; Table 1, Fig. 1; also see Dunham et al. 2007, Isaak et al. 2010). Over 1/3 of the Boise River watershed burned between 1992 and 2003, after a relatively wildfire-free period characterizing most of the 20th century (Burton 2005). Streams that drained watersheds from 1000 to 5300 ha in area were classified into 3 categories according to disturbance history (Dunham et al. 2007). According to records maintained by the Boise National Forest personnel, streams with unburned histories drained watersheds that had no record of wildfire over the past century (Lost Man and Beaver creeks) or had a watershed that was only lightly burned and had little evidence of wildfire a decade after the event (Trail Creek). Watersheds of streams with burned histories were burned extensively (>50%) by stand-replacing wildfire ~10 y before our study (Cottonwood Creek, 1992; Hungarian and Lost creeks, 1994). Streams with burned and reorganized histories (South Fork Sheep, Trapper, and Wren Creeks, 1994) were in watersheds that experienced stand-replacing wildfires followed by small, isolated thunderstorms that triggered channel-reorganizing debris flows and hyperconcentrated floods within 1 wk of the wildfire (Benda et al. 2003; see Dunham et al. 2007 for photographs of the disturbance types). Dunham et al. (2007) reported a correspondence between disturbance history and thermal regime. For a given elevation, streams with the most open canopy (burned and reorganized history) were the warmest, and streams with the most closed canopy (unburned history) the coolest.

Rainbow Trout distribution and abundance

In each of the 9 streams selected for sampling, we established 10 sampling sites at random locations within stream segments (defined by tributary junctions) nested at progressively smaller catchments to a minimum of 400 ha (Table 1, Fig. 1). This stratified random design allowed sampling of longitudinal gradients in these streams while maintaining randomness in the specific location of the site. We used segments with watersheds >400 ha because they were more likely than streams in smaller watersheds to support perennial surface flow in this system.

During summer 2003, we sampled fish with 4-pass-removal electrofishing in sites closed by block nets ~100 m in length to estimate abundance of Rainbow Trout >60 mm

Table 1. Mean (range) characteristics of sampling sites in headwater streams of the Boise National Forest, Idaho.

Stream	No. sites (<i>n</i>)	History	Dates sampled		Site length (m)	Average depth (m)	Maximum depth (m)	Gradient (%)	Elevation (m)
			(dd/mm/2003)	(dd/mm/2003)					
Beaver	10	Unburned	7/15-8/14	105 (85-125)	0.07 (0.05-0.09)	0.37 (0.29-0.60)	4 (3-6)	1386 (1329-1472)	
Trail	10	Unburned	8/1-8/14	98 (95-102)	0.09 (0.05-0.10)	0.46 (0.39-0.55)	4 (2-6)	1544 (1491-1618)	
Lost Man	10	Unburned	9/10-10/2	100 (94-107)	0.10 (0.08-0.15)	0.45 (0.35-0.63)	4 (2-5)	1741 (1565-1863)	
Cottonwood	10	Burned	7/17-7/31	101 (94-108)	0.41 (0.33-0.52)	0.41 (0.33-0.52)	5 (3-8)	1410 (1055-1692)	
Hungarian	10	Burned	8/20-9/11	105 (96-118)	0.11 (0.09-0.15)	0.43 (0.36-0.66)	5 (3-7)	1381 (1289-1495)	
Lost	10	Burned	8/15-9/9	100 (94-114)	0.46 (0.31-0.65)	0.46 (0.31-0.65)	6 (2-12)	1531 (1421-1621)	
Trapper	10	Burned and reorganized	7/14-7/30	106 (101-111)	0.05 (0.04-0.07)	0.35 (0.24-0.54)	5 (4-7)	1519 (1419-1620)	
South Fork Sheep	10	Burned and reorganized	8/6-8/27	101 (95-108)	0.12 (0.08-0.16)	0.58 (0.38-0.82)	12 (8-16)	1486 (1229-1692)	
Wren	10	Burned and reorganized	9/15-9/25	100 (95-105)	0.06 (0.04-0.08)	0.41 (0.27-0.60)	6 (4-8)	1428 (1359-1485)	

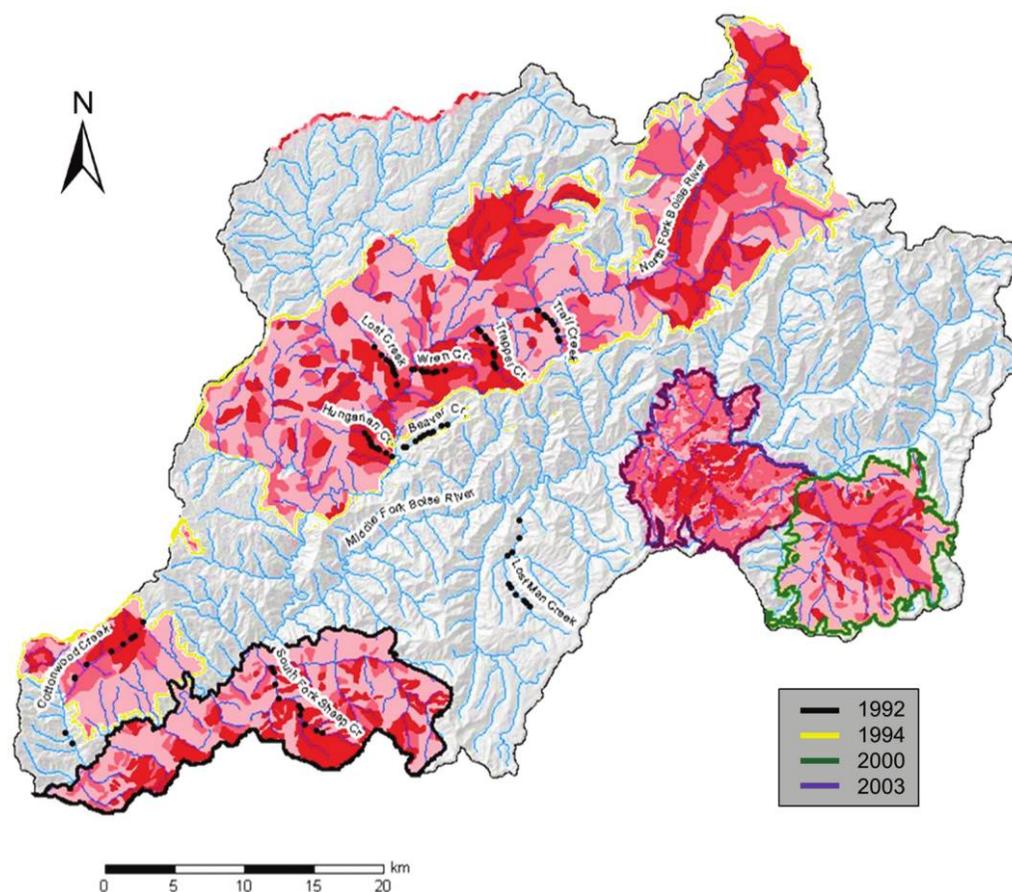


Figure 1. The upper Boise River basin, with shading to indicate elevation and blue lines to represent stream and river systems. Primary river channels and streams selected for sampling are labeled, and closed circles represent locations where Rainbow Trout distribution and abundance data were collected. Wildfire years are indicated by color of outlines around fire perimeters. Intensity of red shading corresponds to fire severity. Spatial resolution of fire severity mapping was greatest for 2000 and 2003 wildfires.

(fork length, FL; see Rosenberger and Dunham 2005 for a more detailed description of fish sampling methods). Streams were sampled by 3 teams in a temporal sequence that avoided confounding time of sampling with disturbance category (Table 1; histories listed as unburned, burned, and burned and reorganized, respectively; early summer: Beaver, Cottonwood, and Trapper creeks; mid-Summer: Trail, Hungarian, and South Fork Sheep creeks; late summer: Lost Man, Lost, and Wren creeks). All individuals captured were tallied, anaesthetized, and measured for FL. We converted counts of Rainbow Trout >60 mm FL to abundance estimates by applying models of 4-pass electrofishing sampling efficiency (Rosenberger and Dunham 2005). We converted abundances to densities (no./m² stream area) based on measurements of average stream width and the total length of stream sampled.

We examined differences in densities among disturbance histories with a mixed-design analysis of variance (ANOVA) with disturbance history as the fixed-effects factor (burned, unburned, and burned and reorganized) and stream ($n = 9$, 3 in each disturbance history) as the

random-effects factor. Densities of age 1+ fish were $\log_{10}(x)$ -transformed to meet normality assumptions, and Scheffé's multiple comparisons were used to examine differences among disturbance types.

Individual characteristics of Rainbow Trout

In early October 2003, we collected 20 Rainbow Trout from each of the 9 streams ($n = 180$). We began single-pass electrofishing 300 m upstream from the confluence of the stream with the Middle or North Forks of the Boise River, with the exception of Cottonwood Creek. The watershed of a small length of stream upstream of the mouth of Cottonwood Creek was only lightly burned; therefore, fish sampling began ~300 m upstream of the downstream extent of the stand-replacing wildfire in this system, which encompassed most of the Cottonwood Creek watershed (Fig. 1). We euthanized Rainbow Trout selected for our study with MS222, then measured, weighed, and dissected them to remove stomach contents and to note stage of maturity. In late autumn, we concluded that indi-

viduals with maturing gonads after the summer growing season were ready to spawn the following spring (assuming overwinter survival). If the individual was maturing, we identified sex. Maturing females had distinctive, uniformly large eggs, and immature females had grainy or clear gonads. Testes of maturing males were milky white and enlarged, whereas immature males had thin, translucent, or transparent gonads.

For lipid content analysis (% dry mass to the nearest 0.01%), we immediately froze 20 individuals/stream in the field with dry ice and sent them to a food laboratory, where lipid content was measured using the acid hydrolysis method (AOAC 1997). Because of the limited sample size, we combined data from streams with a common disturbance history to examine differences among disturbance types in fish lipid content. We used a fixed-effects ANOVA model, with disturbance history and FL of fish as fixed effects and Scheffe's multiple comparisons to examine differences among disturbance histories.

In late September 2004, we revisited a subset of the 9 streams to collect additional information on growth and maturity of individual Rainbow Trout before winter and the spring spawning season (McMillan et al. 2012). Cottonwood (burned history) and South Fork Sheep (burned and reorganized history) creeks were omitted because of logistical and time constraints. As with the lipid analysis, we began sampling 300 m upstream from the stream confluence and proceeded upstream with a single pass. We collected fish, anaesthetized them with MS222, and measured and classified them as immature, maturing male, or maturing female.

We used 2 approaches to obtain data on fish maturation and sex: 1) fish were euthanized with MS 222 and dissected for visual determination of maturity and sex ($n = 284$) or 2) endoscopic examination ($n = 139$; Swenson et al. 2007). Endoscopy is a nonlethal technique, and the primary source of error using this approach is occasional misclassification of immature individuals or maturing females as maturing males (error rate = 5%) because visceral fat can be mistaken for testes using this technique (Swenson et al. 2007). To eliminate this source of error, individuals identified as maturing males through the endoscope were euthanized with anesthetic and dissected to verify the endoscope diagnosis visually.

We obtained information on fish age from autumn collections by removing otoliths and scales from euthanized individuals and scales from individuals released after endoscopy (Murphy and Willis 1996). We verified the accuracy of scale age estimates through comparison with otoliths (100% concurrence; 4 y maximum age). Otoliths and scales were scored independently by 2 observers using a dissecting microscope and lateral light source. In the case of discrepancies in estimated fish age (5% of scale observations), a 3rd observer and consultation between the 2 previous observers resolved all discrepancies.

We used ANOVA (with age as a covariate and Scheffe's multiple comparisons) to examine differences in $\log_{10}(x)$ -transformed length-at-age collected on individual fish in autumn 2004 among disturbance histories. We summarized maturation for fish collected from streams in each disturbance history (streams combined) by age and used a χ^2 test for heterogeneity to examine differences among disturbance histories in % immature, maturing male, and maturing female by age (age 0, 1+, and 2+).

We conducted all statistical analyses in the Statistical Analysis System (SAS/STAT software, version 9; SAS Institute, Cary, North Carolina), with the exception of the mixed-effects ANOVA, which was conducted in Mathematica[®] 8 (Wolfram Research, Champaign, Illinois), and the χ^2 analyses, which were hand-calculated. α -values for statistical significance were set at 0.05.

Individual-based model

We developed an individual-based model (IBM) to investigate if bioenergetic characteristics and territorial feeding behavior of Rainbow Trout could explain the observed pattern that warmer streams contain fewer, but larger, fish. The model also allowed exploration of processes that were difficult to observe in nature, thereby complementing the empirical interpretation of processes gained from field observation.

This model evolved conceptually from the model by Hughes and Grand (2000), which examined the combined implications of growth physiology and the ideal-free-distribution theory of habitat selection. We used the same algorithm used by Hughes and Grand (2000) for allocating limited food among competing, satiable individuals and similar growth and competition submodels (see model description below) to predict patterns in fish size and abundance across habitats with contrasting thermal regimes. However, rather than modeling the patch choice of individuals at a single point in time, our IBM simulated growth and survival over time of individuals competing within fixed patches.

Our IBM did not simulate fish reproduction, complex decision rules (e.g., predator avoidance or swimming costs), or additional environmental variability (e.g., water velocity and depth associated with flow regime) found in other IBMs (e.g., Railsback and Harvey 2002). Instead, predictions emerged only from the competitive interactions of individuals whose growth, mortality, and competitive abilities depended on prior growth. Our model is not appropriate for making absolute predictions of fish size and density in nature because of its deliberate simplicity. Our intent was to apply the model to explore how 2 key mechanisms should affect the relative population and individual responses to different thermal regimes in a simplified environment isolated from the confounding factors of a real stream or other habitat alterations that may occur as a result of wildfire history (e.g., differences in food resources).

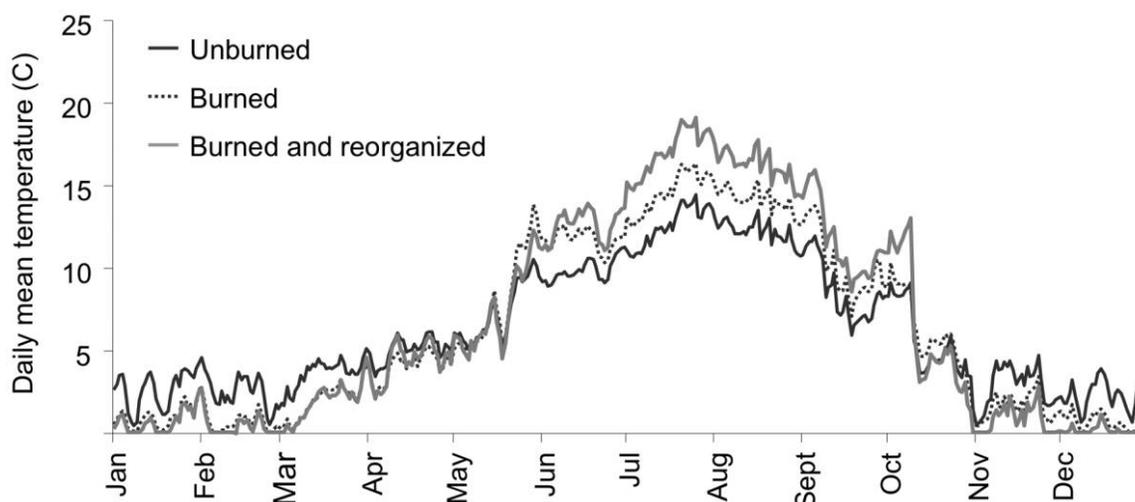


Figure 2. Year-long stream temperature input for the individual-based model representing differences in temperature among unburned, burned, and burned and reorganized headwater streams in the Boise River basin. Ticks on the x -axis represent first day of the month indicated.

The model was implemented in Mathematica 8 (see Appendix S1 for the source code and a pdf file).

We developed temperature scenarios for the 3 modeled burn histories from field data collected from Boise River headwater streams (Fig. 2). We placed temperature loggers (Tidbit™; Onset Computer Corporation, Pocasset, Massachusetts) adjacent to each fish sampling location (10 loggers/stream). For purposes of the simulation, we chose temperature data from a single logger/stream, and we chose 3 sites similar in elevation (unburned: 1309–1473 m asl; burned: 1294–1441 m asl; burned and reorganized: 1271–1416 m asl). We averaged temperature data from mid-June through mid-October 2003 within disturbance history categories ($n = 3$ records/disturbance category) to produce daily summer temperatures representative of each disturbance history. During winter, we monitored temperatures in 1 stream for each disturbance history category: Beaver Creek (unburned; elevation 1285), Lost Creek (burned; elevation 1426), and Trapper Creek (burned and reorganized; elevation 1399). Mean summer values were combined with these winter data to produce a 1-y temperature scenario for each disturbance category. No data were available for September 2 through October 9 and for June 9 through July 1. We filled these gaps via linear interpolation between the values at their start and end.

The model has 3 nonspatially explicit patches, one for each temperature history from 15 May to 14 October. Each patch was initialized with 25 Rainbow Trout with normally distributed wet masses ($\mu = 10$ g, $\sigma = 1$ g) approximating a population of age-1 trout in mid-May based on empirical data. Based on multiple initial simulations, this number of fish was large enough to resolve differences between burn histories and small enough for

timely computation. Each patch received the same set of fish with each model run, assuring that differences in response among patches were not driven by random differences in initial conditions.

The state of each individual trout (wet mass [g] and whether it was alive or dead) was simulated at a daily time step from 15 May until the end of the first calendar year. The daily maximum ration and competitive mass for each fish were calculated from submodels described below. The food in the patch (determined by a constant renewal rate [J/d] that was equal among patches) was allocated among these fish in proportion to their competitive masses. If any fish was allocated more than its maximum ration, the allocation loop was run again to distribute the remainder among the unsatiated fish in the same manner. This loop repeated until all food was distributed or all fish satiated. After the food was allocated, growth was calculated, and a fish ‘died’ if growth declined below a threshold percentage (80%) of its maximum mass. The model recorded all state variables and several derived attributes, such as daily food use, maximum wet mass, and competitive mass, for every fish on every day. Results were observed as plots of the mass, growth, and food use of each individual vs time, or of patch population statistics, such as live fish count and mean fish mass.

The bioenergetics model developed by From and Rasmussen (1984) and Rasmussen and From (1991) was used to predict Rainbow Trout growth as a function of mass, ration, and temperature. The model was calibrated with high-energy-density pellet food, so the estimates of growth on maximum rations were unreasonably large for fish subsisting on natural food (G. Rasmussen, Technical University of Denmark, National Institute of Aquatic Resources, Freshwater Fisheries, unpublished data). To account for

this effect, we incorporated a parameter to limit the maximum daily ration to 30% of the pellet-derived value. This percentage represents the combined effects of factors (e.g., low energy density or low prey encounter rate) that limit energy intake from wild prey compared to pellets (except for competition, which is treated separately). Our focus was on relative differences among thermal inputs rather than absolute predictions of fish length, so we made the simplifying assumptions of indefinite growth and did not assign maturity to individuals.

Competitive mass was modeled as a simple power function of wet mass:

$$\text{competitive mass} = (\text{wet mass})^\gamma. \quad (\text{Eq. 1})$$

In combination with the iterative food allocation algorithm and satiation limits, this equation models a broad continuum of competitive scenarios. At $\gamma = 0$, all fish obtain an equal amount of food until satiated. At large values, such as $\gamma = 100$, subdominant individuals get practically no food unless all larger (more dominant) individuals are satiated. Model output was examined with γ ranging from 0 to >100 , but we selected the value of $\gamma = 2$ because it best

reflects the territorial nature of stream salmonids, in which larger individuals claim better territories, but even poor territories offer some food (Hughes 1992, Keeley 2000).

RESULTS

Rainbow Trout distribution and abundance

Rainbow Trout were the dominant salmonid species ($>95\%$ of salmonids captured) in the study streams and were found in all study sites (Dunham et al. 2007). Bull Trout (*Salvelinus confluentus*) and introduced Brook Trout (*Salvelinus fontinalis*) were sporadically distributed in relatively low numbers. Other species captured included Short-head Sculpin (*Cottus confusus*) and tailed frog larvae (*Ascaphus montanus*).

Density estimates for Rainbow Trout >60 mm overlapped among streams with different disturbance histories. However, examination of length-frequency histograms indicate that young-of-the-year (hereafter, age-0 fish) were growing larger than our 60-mm cutoff by the middle and end of the growing season, particularly in warmer, wild-fire-affected streams (Fig. 3). Therefore, we decided that

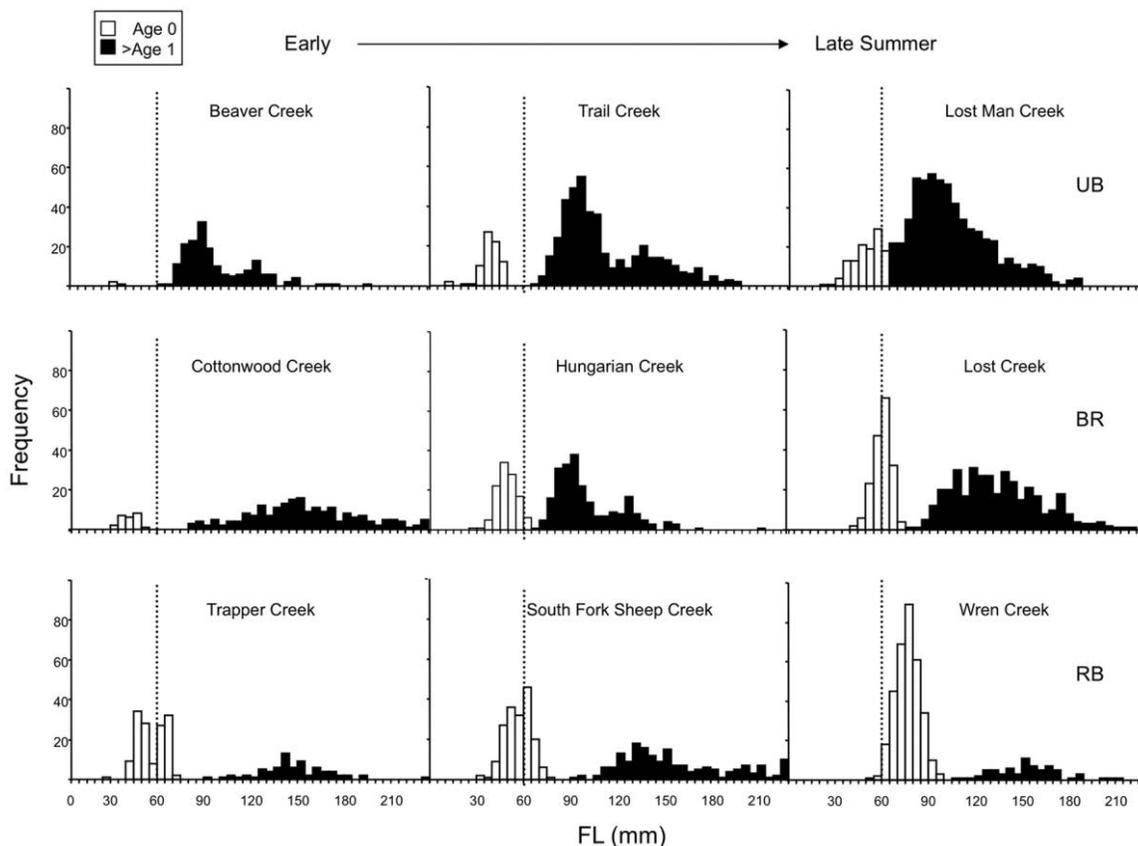


Figure 3. Length-frequency histograms of Rainbow Trout captured in 10 sites (combined) at each of 9 headwater streams in the Boise River basin. Fish >60 -mm fork length (FL) to the right of the dotted line recruit predictably to electrofishing sampling gear (Rosenberger and Dunham 2005). Histograms are organized by disturbance type in rows (UB = unburned, BR = burned, RB = burned and reorganized).

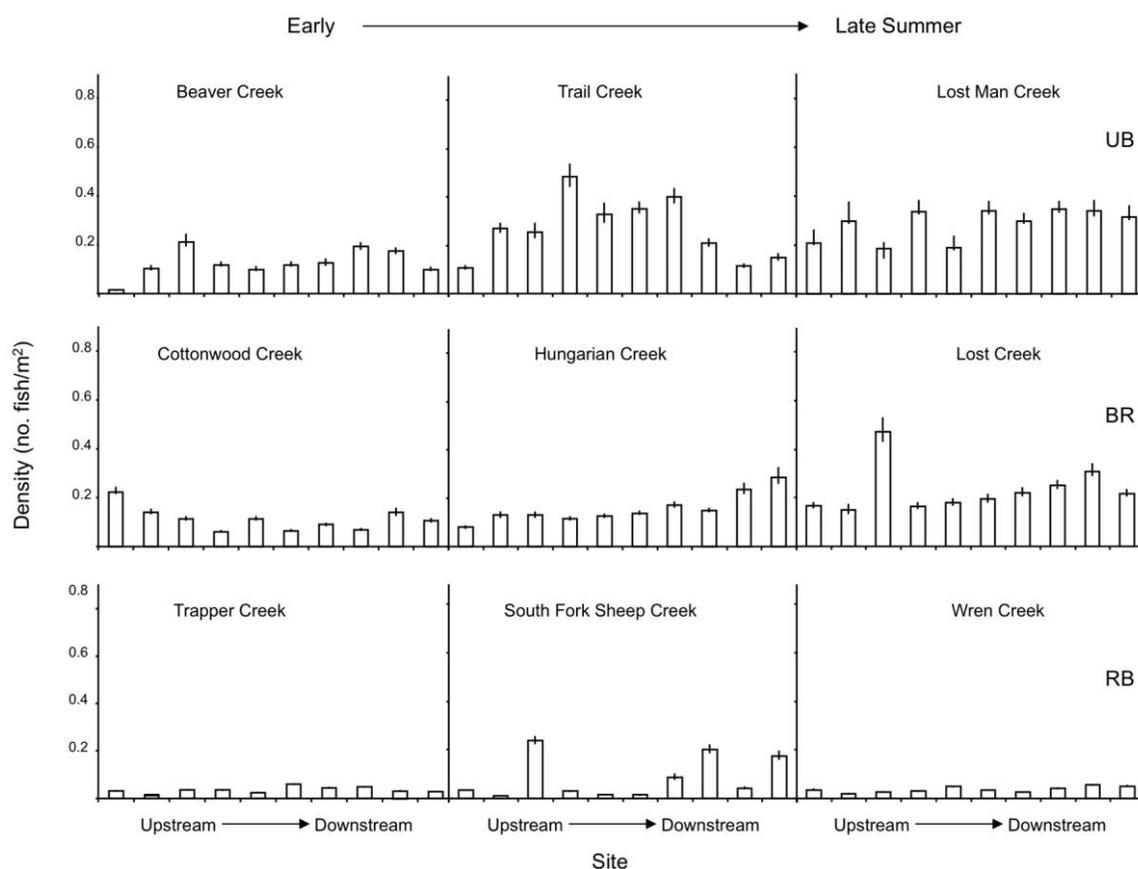


Figure 4. Densities of age-1+ Rainbow Trout (no. fish/m² stream area) in sites ($n = 10$ /stream), ordered from the most downstream to most upstream according to disturbance history (UB = unburned, BR = burned, RB = burned and reorganized). Modeled abundance estimates with 95% confidence intervals (CIs) were used to calculate trout densities (and corresponding CIs).

the 60-mm cutoff was not appropriate for comparisons among streams, and we adjusted abundance estimates to remove probable age-0 individuals (based on cutoffs interpreted from length-frequency histograms; Figs 3, 4).

When we restricted density estimates to probable age-1+ fish, we observed significant differences based on stream disturbance history. Lowest densities occurred in streams with burned and reorganized histories, and highest densities occurred in streams with unburned histories (ANOVA, disturbance history: $F = 68.3$, $df = 2$, $p < 0.001$; stream effect: $F = 4.6$, $df = 6$, $p < 0.001$; Fig. 4). Scheffé's pairwise comparisons indicate that streams with burned and reorganized histories had significantly lower densities of age-1+ fish than did streams with other disturbance histories, but densities did not differ significantly between streams with burned and unburned histories.

Individual characteristics of Rainbow Trout in autumn

Lipid content of Rainbow Trout captured in autumn 2003 corresponded with the disturbance history of the stream of origin and was positively related to FL (General Linear Model, $F = 14.11$, $df = 4$, $p < 0.001$, $R^2 = 0.49$;

disturbance history [class variable]: $F = 17.0$, $df = 2$, $p < 0.001$; FL: $F = 15.7$, $df = 1$, $p < 0.001$). Rainbow Trout in streams with burned and reorganized histories had lower lipid content than Rainbow Trout in streams with burned or unburned histories (Least Significant Means: unburned = 4.67%, burned = 4.97%, burned and reorganized = 4.23% lipid). Fish in streams with burned and reorganized histories had significantly lower lipid content than fish in streams with burned histories ($p = 0.002$).

Fish sampled in autumn 2004 were primarily age-0 and age-1 individuals (Fig. 5A, B). $\log_{10}(x)$ -transformed length-at-age for 0 to 3-y-old individuals differed significantly between disturbance histories (General Linear Model, $F = 204.04$, $df = 4$, $p < 0.001$, $R^2 = 0.67$; disturbance history, $F = 116.7$, $df = 2$, $p < 0.001$; Age: $F = 376.5$, $df = 2$, $p < 0.001$). Trout in warmer streams with burned and reorganized histories had the greatest length-at-age, and trout in cooler streams with unburned histories the smallest (Scheffé multiple comparisons, $p < 0.001$; Fig. 5A).

In autumn, trout in the warmer streams with burned and burned and reorganized histories displayed an earlier onset of maturity (Fig. 5B). Most age-0 individuals were immature, and the proportion of maturing individuals did

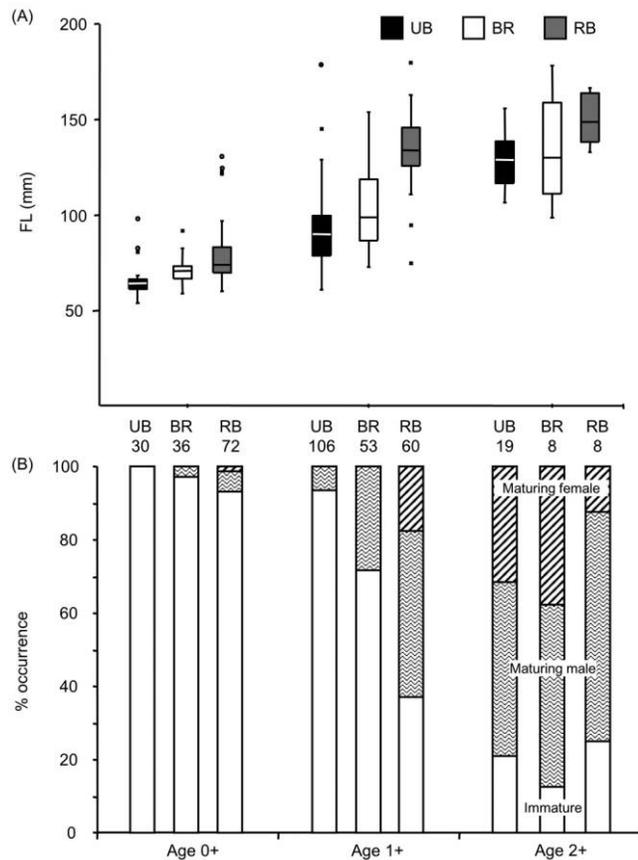


Figure 5. A.—Box-and-whisker plot showing fish fork length (FL) by age class and disturbance history of headwater streams with unburned (UB), burned (BR), and burned watersheds with channel reorganization (RB) in the Boise River basin. Lines in boxes are medians, box ends are quartiles, whiskers represent the interquartile range, and dots are outliers. B.—% occurrence of fish in each age and maturity category captured in UB, B, and BR streams in autumn 2004.

not differ among disturbance histories ($\chi^2 = 2.9$, $p = 0.23$). All age-0 individuals in streams with unburned histories were immature, but we observed a low incidence of maturing males (3 and 6% in streams with burned and burned and reorganized histories, respectively) of this age in all streams with a burned history and 1 age-0 maturing female (verified via otolith age) in a stream with burned and reorganized history (Fig. 5B).

Onset of maturation for age-1 individuals differed among disturbance histories ($\chi^2 = 70.7$, $p < 0.001$; Fig. 5B). Most age-1 individuals in streams with unburned histories were immature (93%), and the incidence of maturing males was low (7%). In streams with burned histories, age-1 maturing males were observed frequently (28%), but no age-1 maturing females were found. In burned and reorganized streams, 17% of age-1 individuals collected were maturing females, and 50% were maturing males. Sample sizes of age-2 individuals were small, particularly for

streams with burned histories, and proportions of individuals in different maturity categories did not differ among disturbance histories ($\chi^2 = 1.6$, $p = 0.45$; Fig. 5B).

Individual-based model

In the individual-based modeling environment, warmer patches corresponding to burned and burned and reorganized temperature regimes contained fewer and larger fish when food supply was not sufficient to sustain every fish in each patch throughout the summer (Fig. 6A, B). This pattern emerged in June, when temperatures were consistently higher in streams with burned histories (Fig. 2). Warmer temperatures resulted in faster growth and greater food use by well fed, dominant trout. Subordinate competitors declined faster than those in cooler water because the dominant individuals left less food and because subordinates lost more mass on poor rations at higher temperatures. The faster growth of dominant individuals and decline of subordinates resulted in larger variance in fish size and growth rate in warmer streams (Fig. 7A–F). Mean size of individual fish did not show a consistent pattern until the late June portion of the simulation because the early decline in small fish roughly compensated for the improved growth of large fish. Subordinate competitors perished earlier in warm streams (mid-July; Fig. 7A–C), and this loss of the smallest individuals decreased the population size and increased mean fish size, generating a ubiquitous pattern that continued throughout the summer simulation (Fig. 6A, B). The death of poor competitors left more food available for all fish unless γ was very large, and this effect slightly strengthened the pattern in fish size.

With enough food to sustain all fish, abundance equalized across patches, and the pattern of larger fish in warmer streams remained. However, this pattern was generated entirely by differential growth rates and not by the higher mortality of small fish. A rare exception to this pattern occurred when there was just enough food to sustain all fish, but not enough for all of them to grow well. Under these conditions, dominant fish had very little advantage. In this scenario, fish grew faster in cooler streams.

DISCUSSION

Rainbow Trout were widespread and continuously distributed in headwater streams of the Boise River basin regardless of the history of wildfire and channel disturbance. The most dramatic and consistent disturbance effect in sampled headwater streams of the Boise River basin is an increase in temperature, concomitant with a decrease in canopy cover (Dunham et al. 2007). This result agrees with published research that suggests Rainbow Trout can thrive in headwater streams after wildfire-related disturbances and consequent alteration of habitat (Howell 2006, Dunham et al. 2007, Sestrich et al. 2011). However, these populations were fundamentally altered by the history of

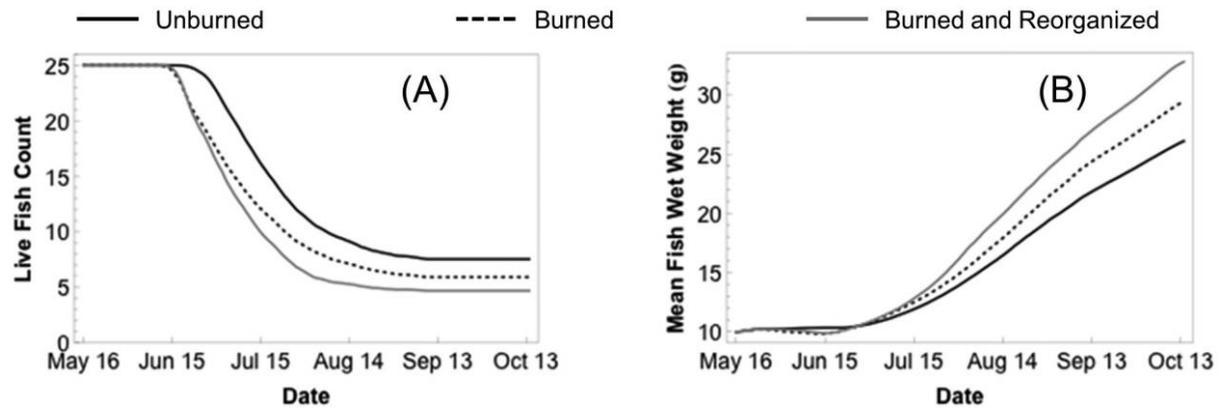


Figure 6. Mean Rainbow Trout abundance (A) and mass (B) over 25 individual-based simulations of 3 temperature regimes associated with disturbance histories of headwater streams with unburned (UB), burned (BR), and burned watersheds with channel reorganization (RB) in the Boise River basin.

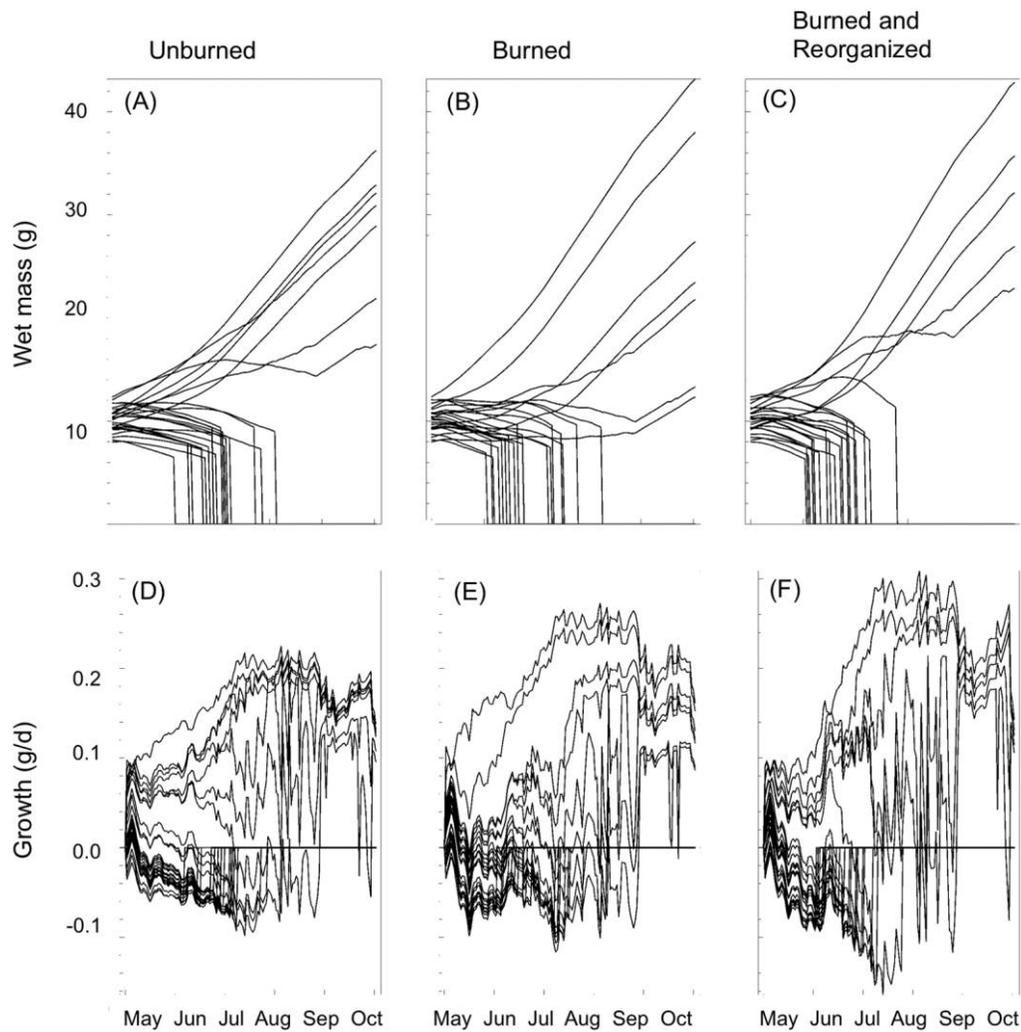


Figure 7. Individual growth histories of age-1 Rainbow Trout in simulations of 3 temperature regimes associated with disturbance histories of headwater streams with unburned (UB) (A, D), burned (BR) (B, E), and burned watersheds with channel reorganization (RB) (C, F) in the Boise River basin. Each line tracks the daily mass (A–C) or growth (D–F) of one of 25 individuals in a representative model run with a constant food supply (21 kJ/d) in each patch and competition exponent $\gamma = 2$ (Appendix S1). A vertical line at the end of an individual's trajectory indicates mortality. The higher variance in daily growth in warmer streams results in earlier mortality of small fish and a larger average mass among fish remaining alive, generating the patterns observed in Fig. 6. Note earlier loss of subordinate individuals in the simulation following a period of negative growth and the increased size of those fish remaining in the burned and reorganized category (C, F).

wildfire in their watersheds. If we considered only older age classes (age-1+), trout abundances were highest in streams in unburned watersheds and lowest in reorganized streams in burned watersheds. We also observed differences in characteristics, including condition, length-at-age, and age-at-maturity, of individual Rainbow Trout among our stream types. Rainbow Trout in the warmest systems with a history of the severest disturbances were larger in size at-age, had lower lipid content, and were maturing earlier compared to those in cooler streams without a history of severe disturbance.

Differences in Rainbow Trout populations among disturbance histories could be caused by multiple factors, including stream channel features, cover, flow regimes, and differences in invertebrate prey resources (Rieman et al. 2005, Rosenberger et al. 2011). We posited that temperature differences among disturbance histories alone could drive observed differences in Rainbow Trout populations based on the interplay of temperature, competition, and bioenergetics. Results from the individual-based model reproduced relative differences among disturbance histories in fish density and size-at-age, even without other plausible mechanisms incorporated into our model (e.g., size-selective predation or differences among stream disturbance histories in food availability). Model simulations showed greater growth disparity between strong and weak competitors in warmer streams, leading to higher mortality of the small fish and a population of fewer, but larger fish. The observed trend in population density follows logically from the greater food needs of faster growing fish in warmer water, potentially combined with the propensity of territorial salmonids to defend foraging locations (Grant et al. 1998). Our model excludes much of the complexity of natural systems (e.g., potential emigration of weaker competitors rather than mortality), but it suggests that the mechanisms we investigated should produce a tendency toward the patterns and relative differences observed among streams with different thermal regimes. However, it does not eliminate the possibility that other factors also may play a role in observed differences among Rainbow Trout.

Our results can be associated with ecological mechanisms that lead to simultaneous changes in environmental conditions and species traits (Warren and Liss 1980). When an environmental characteristic, such as temperature, changes, a species may adapt through altered rates of growth and maturation (Fraker et al. 2002, Morita and Nagasawa 2010, Sloat et al. 2014). Within its optimal range, fish growth tends to increase with temperature if adequate food supplies are available (Brett 1952, 1979, Bear et al. 2007), at a potential cost to lipid levels relative to fish in cooler temperatures within that range (Tocher 2003).

Both growth and lipid content are positively associated with earlier age at maturity for salmonines (Thorpe et al. 1998, McMillan et al. 2012, Sloat et al. 2014), par-

ticularly for males, because fitness is less size-dependent for males than for females (Fleming and Reynolds 2004). We observed larger size-at-age and earlier maturity for both males and females in warmer streams. The observation of a maturing age-0 female Rainbow Trout in a burned and reorganized stream is particularly remarkable. In this case, size acquisition probably was important for the onset of maturity, but lower lipid content of fish in warmer systems could delay maturity (Sloat et al. 2014). Lipid levels in our study were lower overall than observed for this species in other locations (McMillan et al. 2012).

Greater numbers of the age-1 fish are maturing in warmer systems, suggesting a demographic shift in these populations. Our study streams are adjacent to one another in the same drainage (Fig. 1), and the Rainbow Trout populations are not genetically distinct (Neville et al. 2009). Therefore, we suspect that observed differences among individuals reflect phenotypic plasticity of Rainbow Trout under different thermal regimes rather than local adaptation to thermal regimes leading to genotypic differences among populations.

In addition to factors, such as stream flow, cover, or prey resource availability, our model did not include all potential temperature-driven mechanisms that could lead to similar patterns (e.g., reproductive ecology). The differences in FL of age-0 Rainbow Trout among disturbance histories (especially their greater length in warmer streams) may be related to earlier emergence from redds as a result of warmer incubation conditions (e.g., Beacham and Murray 1987, Heck 2007). Furthermore, model results depended critically on the fact that water temperatures never exceeded tolerance levels for Rainbow Trout for extended periods of time. Fish further downstream in these systems may experience such conditions (Dunham et al. 2007), but may be able to migrate upstream during these periods of stress (Wurtsbaugh and Neverman 1988, Breau et al. 2011, Armstrong et al. 2013). If any of the streams, particularly those with severely burned watersheds and reorganized channels, chronically exceed the tolerance threshold throughout the system, we anticipate a different, or less predictable, outcome.

Many investigators who examine effects of habitat alteration on fish populations focus on patterns of fish abundance, density, or distribution, without investigating mechanistic explanations for observed patterns (e.g., Howell 2006, Dunham et al. 2007). By closely examining individual length-at-age, condition, and maturation of Rainbow Trout, we found that a legacy of wildfire and channel disturbance affects fish in a more complex manner than distribution and density responses alone would suggest, particularly if we considered only density estimates of all fish >60 mm in length rather than estimating densities of fish age-1 or older. We suggest that these patterns are largely a result of increased stream temperature, a significant, long-term effect of stand-replacing wildfire on aquatic sys-

tems that can persist through intermediate time scales (i.e., several years to decades; Dunham et al. 2007, Mahlum et al. 2011) and affect the ecology and life history of resident organisms (McMillan et al. 2012, Sloat et al. 2014). We would expect disturbance-related temperature increases to be more detrimental in habitats that were thermally marginal before the disturbance, such as those at the southern edge of the range of Rainbow Trout, and the persistence of those trout populations may require other mechanisms of resistance, such as movement to thermal refugia (Kaeding 1996).

The apparent mechanisms underlying our results should apply similarly to other disturbances that alter stream temperature regimes, from anthropogenic deforestation (Quinn and Wright-Stow 2008) to global climate change (Isaak et al. 2012). Riverine salmonids share the same qualitative relationship between growth, food, and temperature and similar territorial interference competition, so climate change could result in similar demographic shifts in other salmonid populations. We suggest that studies examining implications of climate change or wildfire history for salmonids be focused not only on those areas where temperatures are marginal for survival, but also in systems that do not exceed the capacity of the species to adapt, where plasticity in response and diversity in life history may be key to apparent resilience.

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LITERATURE CITED

AOAC (Association of Official Analytical Chemists). 1997. Official methods and recommended practices. 1996–1997 edition. Association of Official Analytical Chemists, Arlington, Virginia.

Arismendi, I., S. L. Johnson, J. B. Dunham, R. Haggerty, and D. Hockman-Wert. 2012. The paradox of cooling streams in a

warming world: regional climate trends do not parallel variable local trends in stream temperature in the Pacific continental United States. *Geophysical Research Letters* 39:L10401.

Armstrong, J. B., D. E. Schindler, C. P. Ruff, G. T. Brooks, K. E. Bentley, and C. E. Torgersen. 2013. Diel horizontal migration in streams: juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology* 94:2066–2075.

Beacham, T. D., and C. B. Murray. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 44:244–261.

Bear, E. A., T. E. McMahon, and A. V. Zale. 2007. Comparative thermal requirements of westslope Cutthroat Trout and Rainbow Trout: implications for species interactions and development of thermal protection standards. *Transactions of the American Fisheries Society* 136:1113–1121.

Benda, L., D. Miller, P. Bigelow, and K. Andras. 2003. Effects of post-wildfire erosion on channel environments, Boise River, Idaho. *Forest Ecology and Management* 178:105–149.

Bozek, M. A., and M. K. Young. 1994. Fish mortality resulting from delayed effects of fire in the Greater Yellowstone Ecosystem. *Western North American Naturalist* 54:91–95.

Breau, C., R. A. Cunjak, and S. J. Peake. 2011. Behaviour during elevated water temperatures: can physiology explain movement of juvenile Atlantic salmon to cool water? *Journal of Animal Ecology* 80:844–853.

Brett, J. R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. *Journal of the Fisheries Research Board of Canada* 9:265–323.

Brett, J. R. 1979. Environmental factors and growth. Pages 599–675 in W. S. Hoar, D. J. Randall, J. R. Brett (editors). *Fish physiology volume VIII: bioenergetics and growth*. Academic Press, New York.

Brown, D. K., A. A. Echell, D. L. Propst, J. E. Brooks, and W. L. Fisher. 2001. Catastrophic wildfire and number of populations as factors influencing risk of extinction for Gila Trout (*Oncorhynchus gilae*). *Western North American Naturalist* 61:139–148.

Burton, T. A. 2005. Fish and stream habitat risks from uncharacteristic wildfire: observations from 17 years of fire-related disturbances on the Boise National Forest, Idaho. *Forest Ecology and Management* 211:140–149.

Dunham, J. B., A. E. Rosenberger, C. H. Luce, and B. E. Rieman. 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. *Ecosystems* 10:335–346.

Fleming, I. A., and J. D. Reynolds. 2004. Salmonid breeding systems. Pages 264–294 in S. C. Stearns and A. P. Hendry (editors). *Evolution illuminated: salmon and their relatives*. Oxford University Press, New York.

Fraker, M. E., J. W. Snodgrass, and F. Morgan. 2002. Differences in growth and maturation of blacknose dace (*Rhinichthys atratulus*) across an urban-rural gradient. *Copeia* 2002:1122–1127.

From, J., and G. Rasmussen. 1984. A growth model, gastric evacuation and body composition in rainbow trout, *Salmo gairdneri* Richardson, 1836. *Dana – Journal of Fisheries and Marine Research* 3:61–139.

- Grant, J. W., J. K. McKay, S. P. Carroll, and D. N. Reznick. 1998. Implications of territory size for the measurement and prediction of salmonid abundance in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 55:181–190.
- Heck, M. P. 2007. Effects of wildfire on growth and demographics of coastal cutthroat trout in headwater streams. Master's Thesis, Oregon State University, Corvallis, Oregon.
- Hof, C., M. Brändle, and R. Brandl. 2008. Latitudinal variation of diversity in European freshwater animals is not concordant across habitat types. *Global Ecology and Biogeography* 17:539–546.
- Howell, P. J. 2006. Effects of wildfire and subsequent hydrologic events on fish distribution and abundance in tributaries of the North Fork John Day River. *North American Journal of Fisheries Management* 26:983–994.
- Hughes, N. F. 1992. Ranking of feeding positions by drift-feeding Arctic grayling (*Thymallus arcticus*) in dominance hierarchies. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1994–1998.
- Hughes, N. F., and T. C. Grand. 2000. Physiological ecology meets the ideal-free-distribution: predicting the distribution of size-structured populations across temperature gradients. *Environmental Biology of Fishes* 59:285–298.
- Isaak, D. J., C. H. Luce, B. E. Rieman, D. E. Nagel, E. E. Peterson, D. L. Horan, S. Parkes, and G. L. Chandler. 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications* 20:1350–1371.
- Isaak, D. J., S. Wollrab, D. Horan, and G. Chandler. 2012. Climate change effects on stream and river temperatures across the northwest US from 1980–2009 and implications for salmonid fishes. *Climatic Change* 113:499–524.
- Kaeding, L. R. 1996. Summer use of coolwater tributaries of a geothermally heated stream by rainbow and brown trout, *Oncorhynchus mykiss* and *Salmo trutta*. *American Midland Naturalist* 135:283–292.
- Kammerer, B. D., and S. A. Heppell. 2012. Individual condition indicators of thermal habitat quality in field populations of redband trout (*Oncorhynchus mykiss gairdneri*). *Environmental Biology of Fishes* 96:823–835.
- Keeley, E. R. 2000. An experimental analysis of territory size in juvenile steelhead trout. *Animal Behaviour* 59:477–490.
- Lytle, D. A., and N. L. Poff. 2003. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* 19:95–100.
- Mahlum, S. K., L. A. Eby, M. K. Young, C. G. Clancy, and M. Jakober. 2011. Effects of wildfire on stream temperatures in the Bitterroot River Basin, Montana. *International Journal of Wildland Fire* 20:240–247.
- McMillan, J. R., J. B. Dunham, G. H. Reeves, J. S. Mills, and C. E. Jordan. 2012. Individual condition and stream temperature influence early maturation of rainbow and steelhead trout, *Oncorhynchus mykiss*. *Environmental Biology of Fishes* 93:343–355.
- Miller, D. J., C. H. Luce, and L. E. Benda. 2003. Climatic controls on fire-induced sediment pulses in Yellowstone National Park and central Idaho: a long-term perspective. *Forest Ecology and Management* 178:89–104.
- Morita, K., and T. Nagasawa. 2010. Latitudinal variation in the growth and maturation of masu salmon (*Oncorhynchus masou*) parr. *Canadian Journal of Fisheries and Aquatic Sciences* 67:955–965.
- Murphy, B. R., and D. W. Willis (editors). 1996. *Fisheries techniques*. 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Neville, H. N., J. Dunham, A. Rosenberger, J. Umek, and B. Nelson. 2009. Influences of wildfire, habitat size, and connectivity on trout in headwater streams revealed by patterns of genetic diversity. *Transactions of the American Fisheries Society* 138:1314–1327.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637–669.
- Quinn, J. M., and A. E. Wright-Stow. 2008. Stream size influences stream temperature impacts and recovery rates after clearfell logging. *Forest Ecology and Management* 256:2101–2109.
- Railsback, S. F., and B. C. Harvey. 2002. Analysis of habitat-selection rules using an individual-based model. *Ecology* 83:1817–1830.
- Rasmussen, G., and J. From. 1991. Improved estimates of a growth model and body composition of rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792) as a function of feeding level, temperature and body size. *Dana—Journal of Fisheries and Marine Research* 9:15–30.
- Reed, D. C., A. Rassweiler, M. H. Carr, K. C. Cavanaugh, D. P. Malone, and D. A. Siegel. 2011. Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. *Ecology* 92:2108–2116.
- Rieman, B., J. Dunham, C. Luce, and A. E. Rosenberger. 2005. Implications of changing fire regimes for aquatic ecosystems. Pages 187–191 in L. Lagene, J. Zelnik, S. Cadwallader, and B. Hughes (editors). *Mixed severity fire regimes: ecology and management*, Conference Proceedings, November 17–19, 2004, Spokane, Washington. Vol. AFE MISC03. Washington State University Coop Extension Service/ The Association for Fire Ecology, Pullman, Washington.
- Rieman, B. E., D. Lee, G. Chandler, and D. Myers. 1997. Does wildfire threaten extinction for salmonids? Responses of redband trout and bull trout following recent large fires on the Boise National Forest. Pages 47–57 in *Proceedings of the Symposium on Fire Effects on Threatened and Endangered Species and Their Habitats Conference*, Nov. 13–16, 1995, Coeur D'Alene, Idaho. International Association of Wildland Fire, Fairfield, Washington.
- Rieman, B. E., P. F. Hessburg, C. Luce, and M. R. Dare. 2010. Wildfire and management of forests and native fishes: conflict or opportunity for convergent solutions? *BioScience* 60:460–468.
- Rosenberger, A. E., and J. B. Dunham. 2005. Validation of abundance estimates from mark–recapture and removal techniques for rainbow trout captured by electrofishing in small streams. *North American Journal of Fisheries Management* 25:1395–1410.
- Rosenberger, A. E., J. B. Dunham, J. M. Buffington, and M. S. Wipfli. 2011. Persistent effects of wildfire and debris flows on the invertebrate prey base of rainbow trout in Idaho streams. *Northwest Science* 85:55–63.

- Sestrich, C. M., T. E. McMahon, and M. K. Young. 2011. Influence of fire on native and nonnative salmonid populations and habitat in a Western Montana basin. *Transactions of the American Fisheries Society* 140:136–146.
- Sloat, M. R., D. J. Fraser, J. B. Dunham, J. A. Falke, C. E. Jordan, J. R. McMillan, and H. A. Ohms. 2014. Ecological and evolutionary patterns of freshwater maturation in Pacific and Atlantic salmonines. *Reviews in Fish Biology and Fisheries* 24:689–707.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353–391.
- Stanley, E. H., S. M. Powers, and N. R. Lottig. 2010. The evolving legacy of disturbance in stream ecology: concepts, contributions, and coming challenges. *Journal of the North American Benthological Society* 29:67–83.
- Swenson, E. A., A. E. Rosenberger, and P. J. Howell. 2007. Validation of endoscopy for non-lethal determination of maturity of small brook trout. *Transactions of the American Fisheries Society* 136:994–998.
- Thorpe, J. E., M. Mangel, N. B. Metcalfe, and F. A. Huntingford. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology* 12:581–599.
- Tocher, D. R. 2003. Metabolism and functions of lipids and fatty acids in teleost fish. *Reviews in Fisheries Science* 11:107–184.
- Warren, C. E., and W. J. Liss. 1980. Adaptation to aquatic environments. Pages 15–40 *in* R. T. Lackey and L. Nielsen (editors). *Fisheries management*. Blackwell Scientific Publications, Oxford, UK.
- Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences of the United States of America* 108:14175–14180.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayán, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313:940–943.
- Wurtsbaugh, W. A., and D. Neverman. 1988. Post-feeding thermotaxis and daily vertical migration in a larval fish. *Nature* 333:846–848.