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Climate vulnerability for a desert fish: integrating hydrologic exposures, adaptive capacity, and growth potential

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Abstract

Climate vulnerability can be evaluated by multiple organismal responses. We developed a climate vulnerability framework focused on growth potential of redband trout (*Oncorhynchus mykiss newberri*). We employed a bioenergetics model to evaluate spatial variability in growth potential in relation to constraints on body size imposed by stream flow, physiological responses linked to variable thermal regimes, and variation in physiological adaptive capacity inferred from field respirometry. Results indicate that maximum size (g) of redband trout increases with stream discharge. Growth potential is strongly linked to body size, with smaller individuals performing better relative to larger fish in cooler thermal regimes. Annual patterns of growth varied among sites and were related to body size and physiological adaptive capacity. Putatively cold-adapted fish were more likely to exhibit bimodal growth with peaks in spring and autumn, whereas warm-adapted fish exhibit a summer peak in growth potential. These findings offer insights into how climate vulnerability of stream-living fish can be conditioned on both stream flow and thermal regimes, and the potential for physiological adaptive capacity to influence vulnerability.

Key words: bioenergetics, northern Great Basin, Oregon, *Oncorhynchus mykiss newberri*, redband trout, thermal adaptation

Introduction

The effects of climate change on streams include warming temperatures and altered discharge, both of which influence sensitive coldwater species, such as salmonid fishes (Jonsson and Jonsson 2009; Kovach et al. 2016; Crozier et al. 2019). As with many species (Taheri et al. 2021), studies of salmonids often focus on potential changes in species distributions in response to influences of climate change (e.g., Wenger et al. 2011; Bell et al. 2021). Such insights are critical, but by the time changes in species distributions are detected, it may be too late for managers to implement effective climate responses (Sinclair et al. 2010). Here, we consider growth as a more rapid response of fish to stream temperature and discharge. Growth can respond quickly to these influences and is obviously linked to individual fitness, and ultimately population responses (Dowd et al. 2015; Sinclair et al. 2016; Lefevre et al. 2021).

Growth in fishes is often evaluated mechanistically using bioenergetic models (Deslauriers et al. 2017). This approach is well suited to evaluating influences of climate, as temperature is a key factor in bioenergetic models and plays a critical role in driving multiple physiological processes influencing growth (e.g., Beauchamp 2009). Although bioenergetic models can account for influences of stream discharge on swimming costs and foraging success, the additional complexity of adding these components (Jowett et al. 2021) may limit their utility for evaluating influences of climate, as such assessments typically involve broad extents. One factor that can be readily incorporated into broadscale assessments is the potential influence of stream discharge on body size (Harvey and Stewart 1991; Al-Chokhachy et al. 2022). Changes in body size have multiple implications for growth and bioenergetics, including respiration and consumption (Beauchamp 2009; Oke et al. 2020).

In addition to considering climate exposures such as stream temperatures and discharge, it is critical to also consider how variation in the evolutionary potential of a species will impact their vulnerability to climate change (Eizaguirre and Baltazar-Soares 2014). Within a bioenergetic framework, it is possible that local physiological adaptation to historical climate exposures could influence fish growth responses. Salmonids, for example, are well-known to form genetically and geographically distinct, local adaptations (Eliason et al. 2011; Fraser et al. 2011). Accounting for adaptive capacity, physical exposures (e.g., stream temperature and discharge), and sensitivity (e.g., baseline species responses to physical exposures) can provide a more comprehensive understanding of species' vulnerability to climate (Foden et al. 2019).

In this study, we consider climate vulnerability in terms of processes influencing growth for redband trout (*Oncorhynchus mykiss newberri*), a salmonid fish that is known to be sensitive to climate change (Wenger et al. 2011; Warren et al. 2014; Wade et al. 2017). We consider variability in annual thermal regimes to model growth with a bioenergetic model (Benjamin et al. 2020; Armstrong et al. 2021), influences of stream size on body size (Harvey and Stewart 1991; Al-Chokhachy et al. 2022), and physiological parameters from warm- and cold-water-adapted populations (Anlauf-Dunn et al. 2022; Hahlbeck et al. 2023) to estimate the capacity of growth potential. This approach follows the convention of integrating these three factors in climate vulnerability assessments (exposure, sensitivity, and adaptive capacity; Foden et al. 2019) within a widely used mechanistic model of fish growth (Deslauriers et al. 2017).

Specifically, our objectives in this work were to (1) use a bioenergetic model to estimate growth potential in relation to climate-related effects of stream temperature regimes and body size (an indirect effect of stream discharge), (2) apply the model to evaluate spatial variability in growth potential across a broad spectrum of contemporary climate exposures, and (3) account for thermally adapted respiration and consumption rate parameters to influence growth potential across these exposures. The collective insights from this work represent an integrated approache to understanding unique components of climate vulnerability for native trout, which represent a critical resource that is potentially imperiled by warming climates (Kovach et al. 2016, 2019).

Methods

Study region

Our study focused on redband trout in the northern Great Basin (NGB) in south-central Oregon (Fig. 1). Watersheds included were within six species management units (SMU) for redband trout in the region based on designations by Oregon Department of Fish and Wildlife (Meeuwig and Clements 2014). The SMUs align roughly with basic hydrologic basins (HUC8; Fig. 1). Drainages within the NGB are endorheic (part of the closed hydrographic Great Basin), with most water ultimately flowing into lowland playas, wetlands, and lakes. Elevation in the NGB ranges from approximately 1200 m to 3000 m. On average, annual precipitation is about 35 cm at lower elevations and over 100 cm in higher elevations, with snow representing most of the precipitation in the latter. In addition to redband trout, other common native fishes include redside shiner (*Richardsonius balteatus*), speckled dace (*Rhinichthys osculus*), longnose dace (*R. cataractae*), bridgelip sucker (*Catostomus columbianus*), tui chub (*Siphateles bicolor*), and mottled sculpin (*Cottus bairdii*), with other localized endemic species present within individual basins, isolated springs, or other unique locations (Mims et al. 2018; Laramie et al. 2020). Common nonnative fishes include brook trout (*Salvelinus fontinalis*), common carp (*Cyprinus carpio*), smallmouth bass (*Micropterus dolomieu*), largemouth bass (*M. salmoides*), and multiple bullhead species (*Ameiurus* spp.), among others (Laramie et al. 2020).

Framework

The framework we applied is based on climate vulnerability concepts advanced by Kovach et al. (2019) and Foden et al. (2019) and adapted from a bioenergetic modeling approach (Beauchamp 2009). We first considered climate or drought-related exposure in terms of reduced stream discharge, which can result in smaller body size of trout (Al-Chokhachy et al. 2022) and consequences for physiological rates and growth potential (Brown et al. 2004). In a warming climate, environmental exposures from altered thermal regimes are also increasingly important (Crausbay et al. 2017). Thermal regimes strongly influence growth potential (Beauchamp 2009; Benjamin et al. 2020; Armstrong et al. 2021) and contribute additional variability in physiological rates to consider within bioenergetic models. Finally, adaptive variability in physiological rates can also be important in terms of driving climate vulnerability, and we accounted for this using data from field respirometry on redband trout (e.g., Anlauf-Dunn et al. 2022). Collectively, this approach accounts for key hydrologic exposures tied to drought (i.e., low-flow stream discharges), thermal regimes, baseline sensitivity of a species to these exposures, and potential variability tied to the diversity of physiological phenotypes. In sum, this accounts for key components of exposure, sensitivity, and adaptive capacity that are often considered in climate change vulnerability assessments (Foden et al. 2019).

Data sources

To inform our assessment of climate vulnerability of redband trout, we used previously collected data or modeled estimates of fish, discharge, temperature, and thermal adaptation. Each source is described below.

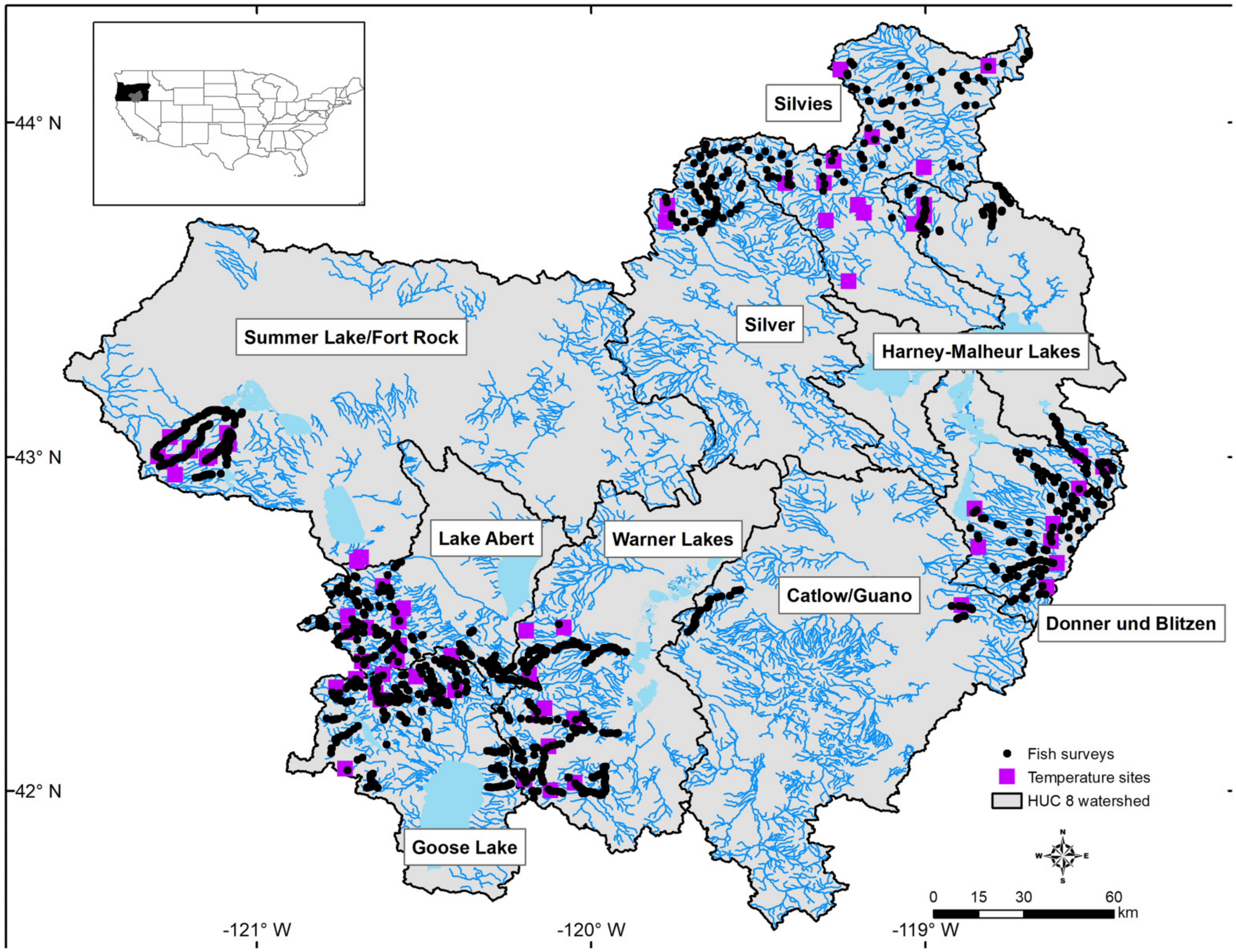
Fish

We used previous fish surveys that were conducted during summer months (June through September) from 2006 to 2012 longitudinally along stream networks (Meeuwig and Clements 2014). The objective of the fish surveys was to quantify the distribution and density of redband trout in the northern Great Basin. Sites were selected based on a generalized random-tessellation stratified (GRTS) design and fish surveys done using depletion or mark-recapture electrofishing (see Meeuwig and Clements 2014 for details). During the time frame, sites were surveyed annually, once or more times. In total, over 1500 sites were surveyed and over 28 000 redband trout were measured (see Laramie et al. 2020 for database of fish observations).

Stream discharge

Stream discharge was taken from monthly estimates provided by a statistical model calibrated with discharge data from U.S. Geological Survey stream gages (Miller et al. 2018*a*, 2018*b*). We matched August discharge estimates with the month and year fish surveys occurred to quantify the poten-

Fig. 1. Northern Great Basin (NGB) in south-eastern Oregon (WGS 1984, decimal degrees) showing fish survey (black circles) locations (Meeuwig and Clements 2014; Laramie et al. 2020) and where water temperature (pink boxes) was measured over a consecutive year (Thorson et al. 2020). Hydrologic unit code names for the nine HUC8 watersheds are labeled. Boundaries, HUCs and stream network lines were from the National Hydrography Dataset (McKay et al. 2012).



tial upper limit of size a fish could achieve under current conditions.

Temperature

Temperature was collected at 124 stream sites across the northern Great Basin and raw data are available in a database (Thorson et al. 2020). A total of 67 sites were used in the analysis. At each of the 67 sites, water temperature was recorded every hour for at least 1 consecutive year during 2016–2019. At two sites, a 5-day gap in temperature occurred; we assumed a linear relationship in temperature between the days when temperature data were missing. We calculated average daily temperature at the 67 sites. The remaining 57 sites were removed from the study because they were observed to be intermittent each year temperature was collected ($n = 37$), temperature was collected for less than one consecutive year ($n = 1$) or sites were outside the range of redband trout ($n = 19$).

Thermal adaptation

For thermal adaptation, we used a previous stream-side respirometry study, which measured oxygen consumption rate ($\dot{M}O_2$ mg O_2 kg^{-1}min^{-1}; see Anlauf-Dunn et al. 2022 for methods) for juvenile redband trout residing in warm- and cold-water streams in the upper Klamath River basin (Hahlbeck et al. 2023). Briefly, redband trout (90–150 mm) were used in three respirometry trials conducted at different initial temperatures ($n = 8$ fish per trial) representing ambient stream conditions, maximum summer conditions, and climate warming conditions. Different temperatures for each trial were chosen for the cold-adapted fish (11 °C, 18 °C, and 22 °C) and warm-adapted fish (14 °C, 22 °C, and 25 °C). Temperature was allowed to fluctuate naturally in the ambient stream conditions trial but was kept constant in the other two trials. After an 18 h acclimation period, fish were chased to exhaustion following standard protocol (Norin and Clark 2016; Little et al. 2020) and air-exposed for

30 sec. Fish were then immediately transferred to chambers instrumented with oxygen probes that measured the rate of metabolic oxygen consumption ($\dot{M}O_2$ mg O_2 kg^{-1}min^{-1}) for 18–24 h (see Anlauf-Dunn et al. 2022). Oxygen consumption was then used to modify consumption and respiration parameters for warm and cold water-adapted fish in the bioenergetic model (see below). Further details and results of the respirometry methods and Klamath River basin study can be found in Anlauf-Dunn et al. (2022) and Halhbeck et al. (2023), respectively.

Analyses

We assumed stream discharge at baseflow was proportional to the upper limit of size a fish could achieve under current conditions (Al-Chokhachy et al. 2022). To understand the relationship of body size of redband trout to the size of the stream occupied we used nonlinear quantile regression. For body size, we estimated the mass (g) of each fish based on their length (mm) from a length–weight relationship in previous study of redband trout in the northern Great Basin ((log(mass) = −4.77 + 2.9 × log(length)); Kunkel 1976). At each site, fish were collected (Meeuwig and Clements 2014; Laramie et al. 2020), we identified the maximum size. For stream size, we used the median August discharge estimates for stream section where fish sampling occurred. We assumed August discharge would represent low discharge for a site. The 90th quantile of the maximum size distribution was used to estimate the upper size a fish could achieve given low discharge. We fit quantile regression models using the “nlrq” function in the “quantreg” package in R (Koenker 2018).

To estimate growth potential of redband trout across sites in the northern Great Basin, we used a bioenergetic model (Deslauriers et al. 2017) with physiological parameters identified by Railsback and Rose (1999). We refer to this as the baseline growth model. Growth in the bioenergetics model is calculated as the difference in energy consumed from energy needed for metabolic costs (i.e., respiration, digestion) and waste (i.e., excretion, egestion), all of which are temperature dependent (Deslauriers et al. 2017).

To account for potential thermal adaptation of redband in the northern Great Basin, we modified physiological parameters used in the baseline model (Table 1). We used results from the previous respirometry study described above for warm- and cold-water juvenile redband trout measured in the upper Klamath River basin(see Table S1 for summarized results). The measured oxygen consumption rate ($\dot{M}O_2$ mg O_2 kg^{-1} min^{-1}; Halhbeck et al. 2023) was used to modify respiration parameters, RQ, RTO and RTM, in the bioenergetic model. RQ is the rate respiration increases over lower water temperatures (i.e., Q_{10}), RTO is the optimal temperature for respiration, and RTM is the maximum or lethal water temperature. Oxygen consumption rate values from the Klamath River basin respirometry experiments were consistent with those measured for redband trout in other south Oregon streams (Rodnick et al. 2004). Consumption metrics were not measured during these stream-side experiments. For modifications in temperature adaptation of consumption parameters in the model, we assumed temperature thresholds in factorial aerobic scope (FAS) from field experiments would identify temperatures when consumption starts to decrease (CTM) and becomes restricted (CTL) (Clark et al. 2013; Farrell 2016). FAS is the ratio between maximum and standard metabolic rates and can be an indicator of limitations to activities such as swimming and foraging (Adams et al. 2022; Eliason et al. 2022). We assumed when FAS reached 3 and 2, consumption would start to decrease and represent CTM and CTL, respectively, in the bioenergetic model.

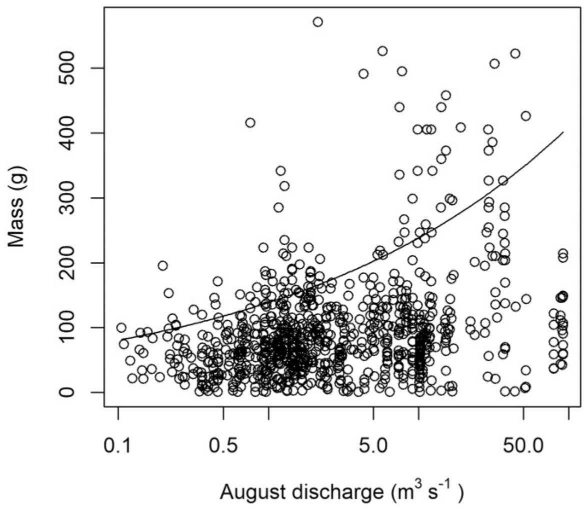
Table 1. Bioenergetic parameters identified for rainbow trout (*Oncorhynchus mykiss*) under baseline; Deslauriers et al. 2017) and adjusted for warm- and cold-water-adapted redband trout populations based on results in Hahlbeck et al. (2023) and Anlauf-Dunn et al. (2022).

Parameter	Baseline	Warm	Cold
RQ	2.2	2.3	2.8
RTO	22.0	22.0	18.0
RTM	26.0	31.0	29.0
CTO	25.0	26.0	22.0
CTM	22.5	22.5	18.0
CTL	24.3	27.5	23.0

Note: Definitions for CTO and CTM were from Railsback and Rose (1999) and differ from those in Deslauriers et al. (2017).

We modeled growth of redband trout at each of the 67 sites with available temperature data. Growth of fish was estimated for 1 consecutive year, starting on 01 January and ending on 31 December. Three starting sizes of fish were used, 10 g (small), 50 g (intermediate), and site-specific upper size limit based on August discharge (large). We assumed the prey quality (energy density = 2800 J·g^{-1}) and quantity (proportion of maximum consumption = 0.4) (Railsback and Rose 1999; Beauchamp 2009) to be identical at each site to allow consistent comparisons among sites. Prey energy density we used was on the lower end of available prey sources in streams (McCarthy et al. 2009); we considered this to be a conservative estimate that could change with stream size (Armstrong et al. 2021). The model allowed us to evaluate growth potential (not realized or actual growth) in response to hydrologic variability (stream discharges and temperatures) with a consistent and simple process-based approach. Accordingly, we did not attempt to account for other processes that could influence growth such as exposure to acute stress (Meeuwig et al. 2004), energy loss due to spawning (Benjamin et al. 2020), activity (Boisclair and Leggett 1989), or a host of other factors that are difficult to account for (Railsback 2022) at a landscape extent. Nor did we evaluate potential for behavioral thermoregulation or other movement-related behaviors to influence environmental exposures (Snyder et al. 2020; Armstrong et al. 2021). The bioenergetic model was run under the three physiological parameter scenarios—baseline, cold, and warm adaptation. We used program R, version 4.1.2 (R Core Team 2021) for all analyses and model simulations.

Fig. 2. Relationship and 90th quantile (line) of August discharge ($m^3 \cdot s^{-1}$) and maximum mass (g) of redband trout in the northern Great Basin, Oregon.



Results

As expected, the mass of redband trout increased with August discharge (90th quantile, $t = 7.59$, $P < 0.01$; Fig. 2). The estimated upper size limit of redband trout in the northern Great Basin ranged from 85.5 g to 364.1 g over a baseflow discharge from 0.1 to 72.4 $m^3 \cdot s^{-1}$. Overall growth potential was greater for smaller sized fish compared to larger fish (Fig. 3). Based on the baseline bioenergetic parameters, small redband trout (starting size of 10 g) had a consistently greater growth potential than intermediate sized fish (starting size of 50 g) or larger fish (site specific starting size). Patterns of growth potential across sizes of fish were similar for the cold-water and warm-water-adapted parameters used (Table S2). These patterns of smaller fish having greater growth potential compared to larger fish were expected and arose from the difference in consumption and energy costs (respiration and waste loss) for different size fish (Fig. 4). Specifically, smaller fish had greater specific consumption rates relative to energy cost at cooler and moderate temperatures than larger fish (Fig. S1).

The annual growth potential of redband trout varied across the northern Great Basin (Fig. 3). Our simulations suggest some sites were not conducive to growth (i.e., growth was minimal or negative), whereas other sites were more favorable to growth. High elevation stream sites tended to have lower annual growth potential compared to lower elevation sites (Fig. S2). Based on visual inspections, streams with lower seasonal variability in temperature had greater growth potential compared to streams with higher seasonal variability (Fig. 5; Fig. S3). We did not attempt to statistically describe these thermal or growth regimes (Falke et al. 2016; Armstrong et al. 2021) and present full-year patterns as a more intuitive way to visualize patterns (Steel et al. 2017).

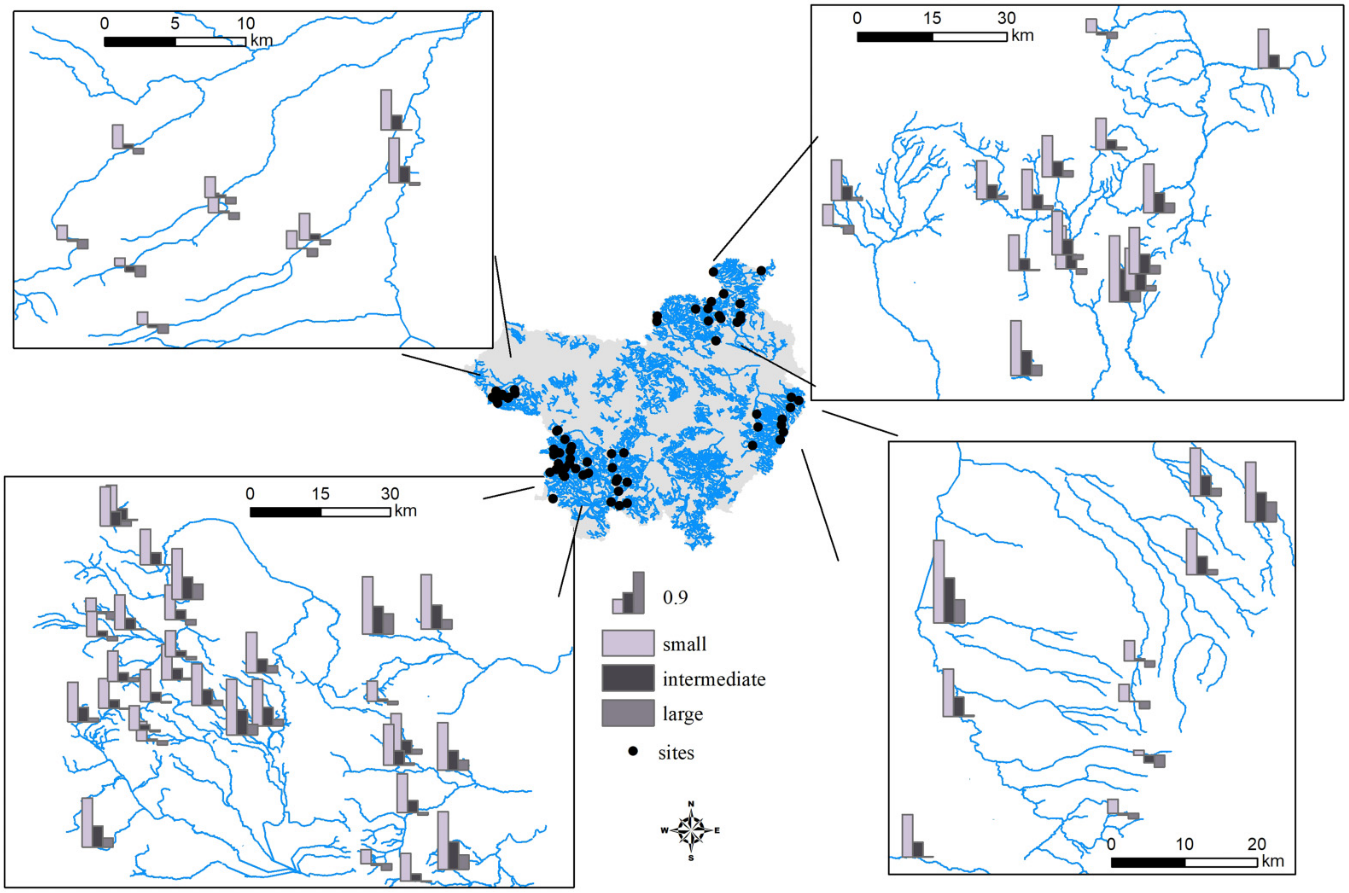
Simulated growth for cold- and warm-water-adapted fish suggested differing patterns in the growth regime over a 1-year period (Fig. 5). Growth for cold-water-adapted fish at many of the sites in the northern Great Basin exhibited a bimodal pattern, with peaks occurring in the spring (approximately days 90 to 150) and autumn (approximately days 250 to 300; Fig. S3). In contrast, growth patterns for warm-water-adapted fish began to peak in the spring and were more likely to remain constant through the autumn. Growth potential was low in the winter for all fish, regardless of physiological characteristics or body size. Patterns of growth for baseline physiological parameters were similar to those presented for the warm-water adapted parameters. Within the parameters used and depending on the size of the adults specific to a site, growth is negative when temperatures reach 21–22 °C for cold-water-adapted fish and 25–26 °C for warm-water-adapted fish (Fig. S1). Warm-water-adapted fish also had negative growth when temperatures were 4 °C or cooler.

Discussion

In this study, we developed a novel mechanistic framework for addressing climate vulnerability of a desert fish that incorporated influences of streamflow on body size, and in turn influences of body size and temperature on growth processes. Specifically, growth processes were considered within a bioenergetic framework (Deslauriers et al. 2017), which allowed us to evaluate how climate vulnerability of growth varied in relation to hydrologic exposures (stream discharge and temperatures). Within this bioenergetic framework we also considered variable respiration parameters. These parameters were derived from field-based respirometry on fish inhabiting streams with contrasting thermal regimes, and thus could represent a range of adaptive variability (Rodnick et al. 2004; Halhbeck et al. 2023). Although we were not able to account for a broad suite of traits influencing climate vulnerability, respiration is a key process influencing net energy gain in fishes and strongly tied to body size (Brown et al. 2004). Implementation of this framework in streams across the hydrologically diverse Great Basin of southeast Oregon provides important insights into spatial patterns of vulnerability for redband trout. The framework also offers a general approach for assessing climate vulnerability with ecologically relevant responses that provide more timely information for managers to act on.

The first step in our vulnerability assessment was to attempt to account for variability in body size in relation to stream discharge. We were able to identify a useful relationship between maximum body size and low-flow discharge. This pattern was expected as a recent analysis of factors influencing body size of trout across North America–identified stream discharge as a major influence (Al-Chokhachy et al. 2022). Within our dataset, however, there was great variability in body size, even for streams with similar low-flow discharge. This indicates there are other factors driving this response and explanations for this variability merit further investigation (Al-Chokhachy et al. 2022). For example, across nearly all low-flow discharges, many sites supported only smaller individuals. This could be due to the sample of fish in a particular site not representing the actual distribution of individual body sizes in a location, errors in discharge estimation, or the influence of local habitat features or landscape

Fig. 3. Estimated annual growth potential (g g^{-1} d^{-1}) based upon baseline bioenergetic parameters (Deslauriers et al. 2017) for redband trout in the northern Great Basin, Oregon (WGS 1984, decimal degrees). Growth estimates are for small (10 g), intermediate (50 g), and large (site-specific) sized fish. Large size for each site was determined by August discharge (Fig. 2). Stream network lines were from the National Hydrography Dataset (McKay et al. 2012).

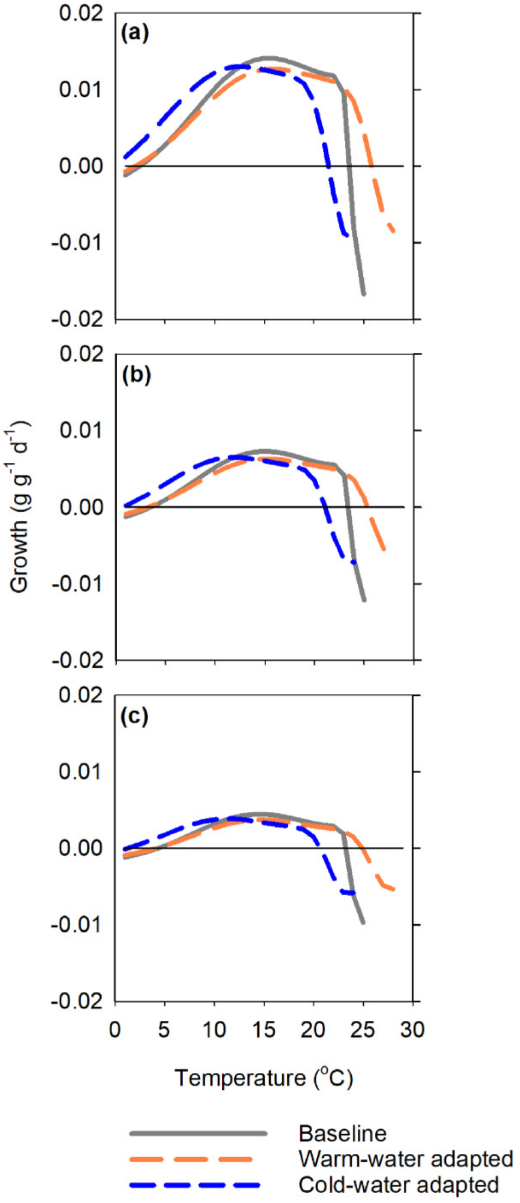


factors (e.g., Armstrong et al. 2021) on body size. Stream size and temperature may also be partially confounded as smaller streams in the Great Basin are often at higher elevations with cooler temperatures (Warren et al. 2014; Isaak et al. 2018), although actual patterns of thermal variability can be very complex (Gendaszek et al. 2020). In addition, the influence of intra- and inter-annual variability of stream discharge on body size was not considered in the current study. Instead, we evaluated three different sizes of fish at each site as a first step in understanding the impact on growth potential. We considered growth as the ecological response in this study, but body size has numerous additional implications (Peters 1986). For example, overwinter survival is linked to body size of younger fish (Smith and Griffith 1994), whereas for adult fish perhaps one of the most important implications of body size is fecundity of females, with consequences for individual reproductive success (Benjamin et al. 2013) and population dynamics (Clements and Ozgul 2016).

Body size was an important driver of growth potential. Annual growth potential of smaller individuals was greater across all thermal regimes. In the coldest streams, larger individuals exhibited negative net energy gain (expressed as growth potential). Although larger individuals have lower specific respiration on a mass-specific basis, their rate of consumption declines relatively faster than combined losses attributable to metabolism and waste (Fig. S1). This results in less energy available to allocate to growth or other functions (Beauchamp 2009). At colder temperatures, the threshold for negative growth potential occurs as a higher temperature for larger fish relative to smaller fish (Fig. S1). Thus, in addition to stream flow, temperature alone is a factor that can constrain body size. Other studies have also shown that redband trout can mature at a smaller size and earlier age where cold-water is associated with presence of higher lipid storage, which may trigger maturation (McMillan et al. 2012), although the full suite of processes that contribute to maturation is not well understood (Sloat et al. 2014).

Within the mechanistic framework we applied, we expected growth potential to be tied to temperature. With year-round temperatures, we were able to evaluate annual growth as well as seasonal patterns by examining daily predictions, adding a level of detail that is often not included in vulnerability assessments (Foden et al. 2019). As reported in other studies of redband trout, thermal regimes strongly influence expected patterns of growth among and within years (McCarthy et al. 2009; Rosenberger et al. 2015; Armstrong

Fig. 4. Temperature-dependent growth for small (10 g), (*a*) intermediate (50 g), (*b*) and large (150 g); (*c*) redband trout under cold-water adaptation, warm-water adaptation, and baseline (Railsback and Rose 1999) parameter values. See Fig. S1 for rates of consumption and energetic costs.

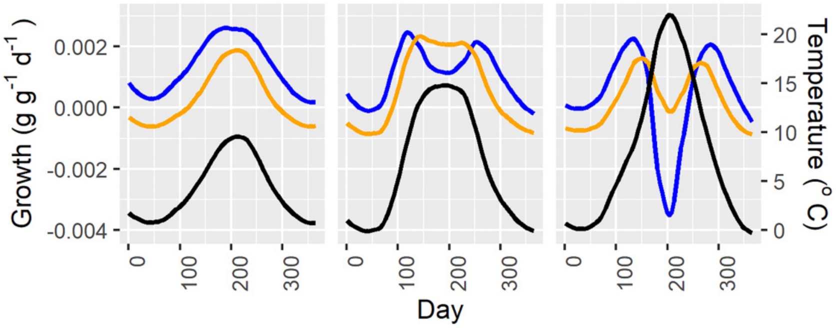


et al. 2021). In this study, we focused primarily on spatial and seasonal variability as we lacked longer-term data to evaluate annual patterns. Although we focused on growth processes at individual sites, most basins we evaluated exhibited broad spatial gradients in available temperatures. This can provide opportunities for fish to use a range of locations (and temperatures) that meet needs across multiple functions and life stages, such as growth (e.g., feeding migrations; Armstrong et al. 2021), survival (e.g., thermal refuges; Snyder et al. 2020), and reproduction (e.g., egg incubation and early rearing; Dahlke et al. 2020). A more continuous survey of thermal conditions in our study basins would be needed to better characterize these conditions (Kovach et al. 2019; Torgersen et al. 2022).

Strong evidence suggests that salmonid populations can be physiologically adapted to their local environments (Eliason et al. 2011; McKenzie et al. 2021) though plasticity (e.g., developmental, acclimatization) can also play a role (Seebacher et al. 2015), and intraspecific variability in thermal tolerance is an important component of vulnerability. After accounting for influences of stream discharge and temperatures on growth potential, we were able to incorporate information on the potential for local adaptation in thermal physiology to influence vulnerability of redband trout. We focused on respiration as a driver of net energy gain or growth potential (Rodnick et al. 2004; Hahlbeck et al. 2023). Since much of the concern over salmonid fishes in relation to climate change is associated with warming stream temperatures (Kovach et al. 2016; Wade et al. 2017), we were interested to know if adaptive physiological variation linked to warming could improve growth potential (Thurman et al. 2020). In our simulations, warm-water-adapted fish continued to have positive growth at approximately 4 °C higher than cold-water-adapted fish. Regardless of thermal adaptations, bioenergetic simulations indicated that the potential for adaptive variation in respiration among redband trout was most likely to increase growth potential for fish exposed to cooler temperatures. This is consistent with the general asymmetry of thermal adaptive capacity in ectotherms (i.e., Jensen's inequality; Martin and Huey 2008). This asymmetry is apparent in plots of modeled energetic costs and gains for redband trout in this study, where a relatively shallow rise in performance with increasing temperature is followed by a rapid drop-off at warmer temperatures.

Although we were only able to address respiration, with respect to this important driver of growth potential, it appears there may be capacity for adaptive variability in respiration to benefit redband trout as stream temperatures warm. Redband trout adapted to warmer temperatures appear to have a higher warming tolerance relative to cold-water-adapted fish (Martin and Huey 2008). Note that some of these physiological differences may also be attributed to plasticity, which could not be distinguished with our study design (Anlauf-Dunn et al. 2022). Additional investigation into more complex patterns of physiological adaptation to warming temperatures may yield more insight into the potential for adaptation to warm temperatures. At present, however, local adaptation to warming offers only limited growth potential for redband trout that remain in place as temperatures warm ("persist in place," Thurman et al. 2020), but there may be opportunities for growth of individuals exposed to warming temperatures through movement within stream networks ("shift in space," Thurman et al. 2020). In this regard, behavioral thermoregulation provides some opportunity for redband trout to exploit complex spatial and temporal variability in stream temperatures (Anderson et al. 2011; Armstrong et al. 2021; Hahlbeck et al. 2021). Over time, however, as streams warm and options for behavioral thermoregulation narrow, it is expected that the diversity of migratory behaviors will decline, and that eventually the species' abundance and distribution will decline (Snyder et al. 2020). Further, as fish distributions

Fig. 5. Daily growth estimates for large redband trout at three representative sites using modified bioenergetic parameters for cold (blue) and warm (orange) temperature-adapted fish and water temperature (°C; black line, secondary axis). Large size was determined by August discharge (Fig. 2). Lines were loess smoothed to show general patterns. See Fig. S3 for growth and thermal patterns for each site.



contract to occupy smaller and more isolated streams, it is expected that declines in body size and spatial fragmentation of habitats may contribute to extinction risk, either in response to slow climate warming or punctuated disturbances associated with climate change such as wildfire and drought (Dunham et al. 2003; Schultz et al. 2017).

Local discharge and temperature regimes can further alter prey availability and quality (Power and Dietrich 2002). In our simulations of growth of redband trout, we kept food resources constant, spatially and temporally, for relative comparisons of growth among sites regardless of local conditions. This is a limitation that has been evaluated in the bioenergetics model (Railsback 2022). There is much to be understood related to availability of food, factors influencing consumption, and consequences for net energy gain. For example, estimates of primary production are related to the density of fish throughout a watershed (Wall et al. 2016; Saunders et al. 2018), yet little is known about the relationship between primary production and variability of food resources across riverscapes (e.g., Bellmore et al. 2013; Benjamin et al. 2022) and how it may influence fish growth and reproductive potential (but see Benjamin et al. 2020; Armstrong et al. 2021). Divergence between food availability and actual feeding may also occur if there are tradeoffs with other influences, such as the threat of predation (Dill and Fraser 1984; Kalb et al. 2018). Evaluation of these and many other factors has occupied an important place in studies of stream-living salmonids for decades (Quinn 2018; Railsback et al. 2021). Future development of the framework we advance here could include more details on these drivers of growth potential.

In a regional context, this study provides an important mechanistic foundation for understanding climate vulnerability of redband trout in the Great Basin and a useful complement to past work that focused on the potential for climate warming to shift species distributions (Wenger et al. 2011; Warren et al. 2014). Persistent drought in the region (Williams et al. 2022) and associated declines in available surface water and cold temperatures (Schultz et al. 2017) are growing concerns for the long-term future of redband trout in the Great Basin (Warren et al. 2014). Whereas there is some opportunity for adaptive capacity (Thurman et al. 2020; Seaborn et al. 2021) to buffer the response of redband trout to these environmental exposures, ultimately it appears that warming and associated fragmentation of stream habitats is the major driver of persistence over the long term for stream-living trout in this region (Dunham et al. 1997; Leasure et al. 2019). As climate-related water scarcity intensifies in the region, managers will face increasingly complex decisions and tradeoffs to balance human and ecosystem needs for water (Crausbay et al. 2017, 2022).

In the broader context of climate change vulnerability assessments, we found that considering a more rapid response (growth potential) in a mechanistic framework (Beauchamp 2009) allowed us to avoid some of the common caveats. Existing vulnerability frameworks are often based on more subjective scoring systems or use simple assessments based on species distributions or climate envelopes (Fortini and Schubert 2017; Foden et al. 2019; Kovach et al. 2019). Although this study focused on a species that is well-known relative to others in the region (Mims et al. 2018), it can hopefully identify key components of climate change vulnerability assessments and information needs for lesser-known species.

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Data availability

The data used in this study are available in ScienceBase as follows: fish (https://doi.org/10.5066/P9QZGDMB), temperature (https://doi.org/10.5066/P924MOCB), and discharge (https://doi.org/10.5066/F7CC0ZMG). The bioenergetics model and parameter inputs for rainbow trout are available at http://fishbioenergetics.org/.

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The authors declare no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2022-0280.

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