Warming exacerbates density dependence

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Increasing water temperatures exacerbate the potential for density dependence in juvenile steelhead

Knut Marius Myrvold[1*]; knut.marius.myrvold@gmail.com

Brian Patrick Kennedy[1,2]; kennedy@uidaho.edu

[1]Department of Fish and Wildlife Sciences

[2]Department of Biological Sciences and Department of Geological Sciences

University of Idaho, Moscow, ID, USA 83844-1136

* Correspondence author: Knut Marius Myrvold, email: knut.marius.myrvold@gmail.com, phone: +47 920-64-963. Present address: Norwegian Institute for Nature Research, 2624 Lillehammer, Norway.

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Abstract

We study the potential effects of predicted climate change on the energetic demands of juvenile steelhead (*Oncorhynchus mykiss*) and their consequences for local population size and structure in Idaho, USA. Projected increases in water temperature incurred on average a 10% higher energetic cost by 2040 (range 7.0%-12.5% among study reaches in the watershed), and a 16% increase (range 8.5%-21.3%) by 2080 following the A1B scenario. The predicted increase in energetic cost was largest in the coolest stream reaches, where the proportional increases in energetic cost exceed that of temperature. Energetically, and in absence of increases in food supply, local densities were consequently expected to decline. We examined which factors best described the shape of current size distributions to explore future size distributions as temperatures increase. Mass distribution skewness was best explained by local biomass (positive relationship) and water temperature (negative relationship). The results suggest that local steelhead cohorts will approach a platykurtic, slightly negatively skewed distribution with increasing temperatures, and demonstrate that temperature can exacerbate demographic density dependence in fish populations.

Introduction

In the face of global warming, local environments are changing at a rapid pace. In turn, the shifts in habitat conditions can influence the ecology and phenotypic expression in the species inhabiting those environments (Parmesan 2006; Rijnsdorp et al. 2009; Crozier and Hutchings 2014). Because fishes are ectotherms they are sensitive to changes in temperature (Rijnsdorp et al. 2009; Crozier et al. 2010). A number of studies have investigated the potential impacts of climate change on salmonids (*Oncorhynchus*, *Salmo*, and *Salvelinus*) in the northern hemisphere, where most freshwater systems are expected to become warmer (Beer and Anderson 2013; Chang and Psaris 2013). Salmonids are coolwater species and may therefore show early responses to warming water temperatures (Wenger et al. 2011; Kovach et al. 2016). Potential impacts on salmonids and their habitats due to warming water temperatures include increased levels of physiological stress and disease (Cooke et al. 2012; Al-Chokhachy et al. 2013), changes in life-history expression (Crozier et al. 2008; Rich et al. 2009; Benjamin et al. 2013; Hegg et al. 2013), range shifts (Ruesch et al. 2012; Cheung et al. 2015; Isaak et al. 2016), concurrent changes in disturbance regimes (Isaak et al. 2010), and altered interactions among species (Wenger et al. 2011).

Importantly, abiotic factors can modulate how demographic density dependence is manifested in populations (Lundberg et al. 2000; Buckley et al. 2010; Crozier et al. 2010; Myrvold and Kennedy 2015a). For example, Crozier et al. (2010) found that the average size of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) was positively related to water temperature at low population densities, but negatively related to temperature at high population densities. At the population level, Myrvold and Kennedy (2015a) found that cohorts of juvenile steelhead (*O. mykiss*) exhibited steeper self-thinning curves in locations with higher temperatures, demonstrating that temperature exacerbated density-dependent regulation of the cohorts. Here, increased energetic demands due to higher temperatures were reflected in higher mortality rates (Myrvold and Kennedy 2015a), a pattern that can be expected from metabolic theory (Brown et al. 2004). The interacting effects of temperature and density dependence can hence be particularly important in fishes, whose energetic demands scale predictably with temperature and body mass (Brett 1971).

Most natural populations exhibit skewed size frequency distributions (Pfister and Stevens 2002; Begon et al. 2006). Individual size disparities (which lead to skewness in size distributions) can be particularly visible in fishes because they exhibit flexible and indeterminate growth (Rubenstein 1981; Nakano 1995; Rose et al. 2001). Importantly, the shape of the size distributions, particularly when hatch dates are synchronized, can provide information about the intensity of intraspecific competition in the population relative to the constraints of their environment (Lomnicki et al. 1999; Pfister and Stevens 2002; Begon et al. 2006; Connolly and Brenkman 2008; Ohlberger et al. 2013). Greater competition typically leads to greater size inequality and positively skewed distributions, whereas less competition relative to the direct constraints of the environment leads to lesser size inequality and negatively skewed distributions (Figure 1; Pfister and Stevens 2002; Begon et al. 2006). For example, most individuals in a sparse population of territorial fishes may be able to fulfill their resource demands without much interference competition, but the larger individuals can be limited by total resource availability relative to their energy expenditure. Here, food availability, and not an individual’s ability to acquire food, might create a negatively skewed size distribution. Hence, by comparing size distributions across gradients of environmental conditions and population density (a proxy for competition) at equal points in time, it can be possible to detect the patterns of skewness, and subsequently infer the processes responsible (Figure 1).

In this article, we demonstrate how predicted temperature increases can elevate individual energetic demands during the warmest period of the year, and in turn, investigate how this may influence population size and structure in juvenile steelhead rearing in the Snake River Basin, United States. Steelhead spend their first years in their natal streams where they compete for food and space, and migrate to the ocean once they reach a certain size (Keeley 2001; Quinn 2005; Kendall et al. 2015). Previous work in the system has shown that temperatures in the summer can approach the thermal tolerance of steelhead, and thus pose an important constraint on individual performance and population dynamics (Myrvold and Kennedy 2015a, b). Our first objective is to quantify the added energetic cost for individuals as incurred by projected warming of water temperatures across the entire size range of juvenile steelhead in their natal rearing habitats. Secondly, we calculate the total energetic demands of local populations across the observed water temperature range in the watershed, and impose the temperature increases to quantify the added energetic requirements associated with predicted climate change. Finally, we compare the shapes of the size distributions across the naturally occurring gradient of population densities and temperature, and discuss how local size distributions might shift in the face of predicted climate change.

Methods

Study area

The study took place in the 694 km^2 Lapwai Creek watershed, Idaho, United States. The watershed is located at the transition between the Columbia River Plateau and the Northern Rockies ecoregions (McGrath et al. 2002), and spans a gradient of land cover and land use from its headwaters on Craig

Mountain (elevation 1530m) to its confluence with the Clearwater River (elevation 237m). The four main tributaries are designated as critical habitat for a wild steelhead population (NMFS 2010), for which no hatchery supplementation exists. As part of a monitoring program to identify drivers of individual performance and population dynamics (Hartson and Kennedy 2015; Myrvold and Kennedy 2015b, c), we established an array of randomly selected study sites representative of the physiographic variation in the watershed (Figure 2). The study sites were approximately 100m long, and key characteristics are given in Table 1 and in Myrvold and Kennedy (2015a). Historically the hydrograph has predominantly resembled a snowmelt-driven pattern, by which most of the precipitation came in the form of snow in the winter and a gradual snowmelt in the spring-early summer (Mote et al. 2003). With predicted climatic change, the region is expected to experience substantial warming over the next decades, due to higher air temperatures and shifts in the amount, form, and timing of precipitation (Mote et al. 2003; Mote and Salathe 2010).

Steelhead data

Data on the size distribution of juvenile steelhead were obtained monthly from each study site from June to October 2011. We captured fish via three-pass depletion electrofishing using a Smith-Root LR-24 backpack electrofisher (Smith-Root Inc., Vancouver, Washington, USA). We measured fork length in millimeters and mass to the nearest decigram. We considered sampling visits where we caught eight or more individuals, and the frequency distribution was binned by 1 g increments. Individuals were classified as *subyearling* (hatched in May the same year) or *overyearling* (hatched in a previous year) based on size frequency histograms at the sampling visit. To separate out effects of ontogenetic changes and life-history decisions (Benjamin et al. 2013) we focused primarily on subyearlings in this analysis. We estimated the size of the subyearling cohort using Carle and Strub's (1978) maximum weighted likelihood estimator for removal data. We then multiplied the estimate with the average mass of subyearlings to obtain the standing biomass present at the sampling visit. To allow for comparison between sampling sites we divided the population estimate and the biomass by the area sampled to obtain density (number/m^2) and biomass per unit area (g/m^2). All sampling and handling procedures were permitted as part of the Section 7 consultation for the Lewiston Orchards Biological Opinion (NMFS 2010), and reviewed by the Idaho Department of Fish and Game and the University of Idaho Institutional Animal Care and Use Committee.

Temperature data

Stream temperatures were recorded every 30 minutes in each study site from 2010 through 2012 using HOBO TidbiT v2 temperature loggers (Onset Computer Corporation, Pocasset, Massachusetts, USA). The temperature data were used 1) to inform climate projections with the observed spatial heterogeneity in the watershed, and 2) to explain variation in the shape of the size distributions of steelhead in each study site.

Temperature projections

We used the NorWeST Regional Database and Modeled Stream Temperature model (Isaak et al. 2010) to predict the future temperatures in the study sites in the Lapwai Creek watershed. The stream temperature model is based on an extensive grid of temperature measurements, and creates continuous temperature profiles (expressed as the average temperature for the month of August) for streams in the region using spatial statistical network models. Between locations where water temperature measurements were made the model interpolates predictions based on characteristics such as elevation, stream order, and discharge (Isaak et al. 2010). The projections are based on the commonly used A1B scenario (Isaak et al. 2010), which emphasizes a balance between fossil- and non-fossil based energy sources (IPCC 2000). The model captures the temperature profile patterns well on the scale of kilometers, but does not account for thermal heterogeneity on smaller spatial extents, e.g. due to spring inputs or groundwater exchange (Snyder et al. 2015). The concordance between the predicted current temperature and our own temperature measurements in the Lapwai Creek watershed was overall very good (average August temperatures of 17.30°C and 17.31°C, respectively), but with local discrepancies (average 0.026°C, SD=0.51; Table 1). We therefore adjusted the projections for the study sites with our local temperature measurements, that is, the temperature increases (predicted future temperature minus predicted current temperature) were added to our measured data, not to the predicted current temperature from the Isaak et al. (2010) model. We considered the projected August temperatures for the 2040s (midpoint for the 2030-2059 period) and 2080s (midpoint for the 2070-2099 period).

Bioenergetic model

We used Fish Bioenergetics 3.0 (Hanson et al. 1997) to model the energetic cost incurred by the water temperature on juvenile steelhead. Bioenergetic models consist of a set of mass-balance equations, which link fish physiology with the environment (Hewett and Kraft 1993; Hanson et al. 1997). Myrvold and Kennedy (2015b) parameterized a detailed bioenergetics model with field values for the Lapwai Creek system, and the following analyses draw on this model. Energetic cost was calculated as the daily energetic demand under a given temperature with no somatic growth, i.e. the cost of maintaining standard metabolism (Hewett and Kraft 1993; Myrvold and Kennedy 2015b). Two main patterns are important for the following analysis (Figure 3). First, standard metabolism is nonlinearly related to temperature, and, secondly, mass-specific metabolism ($J \cdot g^{-1} \cdot d^{-1}$) decreases with fish mass (Myrvold and Kennedy 2015b).

Total energetic demands in local populations

We selected three study sites (USU, ULL, and UML) which spanned the gradient of current temperatures (the lowest, mid, and highest water temperatures in the watershed, respectively), and characterized the population size and structure in each. We then calculated the current and future ration (g prey with an energy density of 4324 J/g; Myrvold and Kennedy 2015b) for maintenance metabolism for each individual for the month of August 2011 in each site. We then compared the sites with regards to the total energy demands necessary to maintain body mass.

To identify the temperature at which metabolic demands start to decrease on the margin (i.e. a change in concavity) we fit a third order polynomial function to the relationship between maintenance consumption rate and temperature up to the maximum predicted temperature for the 2080s scenario (22.45°C). We then took the second-order derivative to find the inflection point, and solved for temperature by setting the function equal to zero.

Shape of subyearling size distributions

We focused the analysis on subyearling steelhead in their first summer (June – October) to avoid the confounding effects of migration. In the Lapwai Creek watershed, steelhead outmigrate at ages 1-3 depending on local factors such as density and habitat productivity (Hartson and Kennedy 2015). Following emergence from the redds (typically the month of May in this system; Taylor et al. 2016) fry disperse in search for suitable shelter habitat, and later establish feeding territories. Mortality is high during this time, and the analysis concerned the period after fry dispersal. We calculated the skewness of the size distribution using the adjusted Fisher-Pearson standardized moment coefficient in SAS 9.2 Proc Univariate (SAS Institute, Cary, North Carolina, USA). The coefficient is unbound and measures the tendency of the deviations to be larger in one direction than in the other. For example, a normal distribution of individuals has a skewness of zero, whereas a distribution with a positive skew (long tail on the right) indicates that there are many small and a few, larger individuals. To quantify how much of the variation in sample skewness attributable to the different levels in the data (sampling visit and study site) we performed a one-way analysis of variance (Raudenbush and Bryk 2002). The model for the variance components for the site- and visit levels (also known as the empty or unconditional model) is expressed as

$$skewness_{ij} = \gamma_{00} + u_{0j} + r_{ij} \text{ (eq. 1)},$$

where γ_{00} is the grand mean skewness of all sampling visits, u_{0j} is the random site effect, i.e. the deviation of site j from the grand mean, and r_{ij} is the random sampling visit effect, i.e. the deviation of visit ij from the site mean. Because sites and sampling visits were randomly sampled from a larger statistical population of potential sites and visits we can assume that $u_{0j} \sim N(0, \tau_{00})$ and $r_{ij} \sim N(0,\sigma^2)$ (Raudenbush and Bryk 2002). The variance decomposition revealed substantial clustering by study site (as indicated by the intraclass correlation coefficient ρ - Table 2), and we hence modeled the skewness under a mixed-effects framework (Raudenbush and Bryk 2002). We investigated the effects of density, biomass, average mass, and water temperature on skewness as these factors have been shown to affect both individual growth and cohort regulation in the system (Hartson and Kennedy 2015; Myrvold and Kennedy 2015a, c, d). A visit-level model of skewness as a function of a visit-level variable *X* (i.e. density, biomass, average mass, and temperature) can be written as

$$skewness_{ij} = \beta_{0j} + \beta_{1j}X_{ij} + r_{ij} \text{ (eq. 2)}$$

To allow for site-specific intercepts, we can write

$$\beta_{0j} = \gamma_{00} + u_{0j} \text{ and } \beta_{1j} = \gamma_{10}$$

Combining into eq. 2, this model structure becomes a random intercept model

$$skewness_{ij} = \gamma_{00} + \gamma_{10}X_{ij} + u_{0j} + r_{ij} \text{ (eq. 3)}$$

Adding more variables to equation 3 expands the model linearly. In addition to the skewness, we were interested in understanding how biomass affected the height of the central peak in the size distribution. We modeled the kurtosis of the size distributions as a function of biomass, using the same framework.

We used SAS 9.2 Proc MIXED specified with the Kenward and Roger (1997) approximation of denominator degrees of freedom and maximum likelihood as the estimator in all the analyses. Models were ranked using the small-sample corrected version of Akaike’s Information Criterion (Akaike 1973; Hurvich and Tsai 1989); the model with the lowest *AICc* value is the best approximating model of the data (Burnham and Anderson 2002). We report on models with substantial relative support, i.e. within 2.0 *AICc* points from the best model, and present their Akaike weight, which is the relative support for a given model in the candidate set (Burnham and Anderson 2002).

Results

Objective 1: Increases in energetic cost

Stream temperatures in the Lapwai Creek watershed were estimated to increase on average by 1.81°C by the 2040s (the midpoint of the period 2030-2059), and by 3.11°C by the 2080s (the period 2070-2099) following the A1B scenario (Table 1). On a site-by-site basis, the predicted percent increase from the current temperature decreased with higher current temperature (Table 1).

We predicted the associated increases in August energetic cost for a size range of juvenile steelhead for each study site (Table 3). Compared to current conditions, the projected temperature increases would on average lead to a 10% higher standard metabolic cost by the 2040s, and a 16% increase by the 2080s. The variation among the study sites in the watershed ranged from 7.0% to 12.5% in the 2040s projection, and from 8.5% to 21.3% in the 2080s projection.

The predicted increase in energetic cost was negatively related to current temperature (Figure 4). In other words, fish in the warmest reaches in the watershed were predicted to have the lowest rate of *increase* in standard metabolism. The reason is that the maintenance metabolic cost decreases more rapidly on the margin at higher temperatures within the thermal tolerance levels (Figure 3). The projected temperature increases (absolute values) in all the study sites were within 2.0% of each other for the 2040s (range 9.5%-11.4%; Table 1), whereas the associated increases in metabolic cost were 7.0% to 12.5% (Table 3, Figure 4). The largest predicted increases in metabolic cost were therefore found in the currently coolest sites. Hence, even though the range of temperature increases were subtle across the study sites (range 1.78°-1.86°C), the energetic impacts of these increases depended upon the actual temperature, present and future (Figure 5). The same pattern, but with larger absolute increases, was visible for the predicted 2080s situation. The inflection point for the temperature-metabolic cost relationship was at 18.0°C (range 17.9°-18.1°C) across the size range of juvenile steelhead.

Objective 2: Total energetic demands in local populations

We calculated the maintenance ration (total mass of prey) necessary for the individuals in three local populations to maintain their body mass. The three study sites (USU, ULL, and UML; Table 4) spanned the observed temperature gradient in the watershed, and included both subyearling and overyearling fish. For example, in order to maintain the body mass for the 61 individuals in USU a total of 1026 g prey was needed for the month of August (Table 4). If the abundance were the same in 2040, this amount would be 1153 g, an increase of 12.4% due to the increases in water temperature. It follows that if the temperature increase were compensated by a 12.4% increase in food availability (in caloric terms) there would be no change in steelhead numbers through mortality or emigration, or reduction in average mass through individual weight loss. This is equivalent to an additional 127 g, or 549 kJ (i.e. 127 g × 4324 J/g) of prey for the month of August. The largest predicted increase in metabolic demands was in the coolest site (USU) and the smallest predicted increase was in the warmest site (UML), consistent with the above reported results for the size range.

In absence of a proportional increase in prey availability, fewer individuals would be supported by the environment due to the increased individual energetic demands. The reduction would be larger in the relatively cooler sites. We further quantified the shape of the size distributions in all the study sites to explore how this would manifest in local abundance and size structure.

Objective 3: Shape of subyearling size distributions

The shape of the size distributions of subyearling steelhead was overall positively skewed (longer tail on the right). Summary statistics for the month of August are given in Table 5. The overall skewness in the size distribution data (all visits combined) was 0.617 (SE=0.092), with 70% of the variance attributable to factors on the visit (residual) level and 30% attributable to factors on the site level (Table 6, top half).

When modeling the factors that could explain the variation in skewness we found that biomass (positive relationship) was the best approximating model (Akaike weight=0.38), with some additional support to water temperature (negative relationship, Akaike weight=0.16). Biomass explained some 28% of the site-level variance and 3% of the visit-level variance. This means that sites with relatively higher biomass and cooler temperatures had positively skewed size distributions, i.e. with longer tails on the right. This corresponds to a situation with many small and a few large individuals (see below). Sites with relatively higher temperatures and lower biomass approximated a normal distribution or had negative skew. In the negatively skewed populations there were relatively more large individuals and fewer small individuals (Figure 6).

Biomass is a composite measure of density and average mass. However, it can be desirable to separate out the relative contribution of these constituents. Using the same approach as described for skewness, we modeled the relationship between biomass and density and average mass, respectively. We found that biomass was largely driven by variation in density (estimate=3.9, *SE*=0.41, *d.f.*=28.4, P(|*t*|)<0.0001, *AICc*=23.5) and less by average mass (estimate= 0.022, *SE*=0.013, *d.f.*=58.8, P(|*t*|)=0.089, *AICc*=67.6).

Finally, there was a positive effect of biomass on the kurtosis of the size distribution with site as a random effect (estimate=0.975, *SE*=0.45, *d.f.*=51.2, *P*(|*t*|)=0.033). This means that the mass distributions in high-density sites tended to be more leptokurtic (narrowly peaked), and conversely, that mass distributions in low-density sites were more platykurtic (flatter and wider; Figure 6).

Discussion

In order to forecast the effects of climate change on fish populations there is a need to identify the potential mechanisms that link the physical environment with biological processes (Brown et al. 2004; Rijnsdorp et al. 2009; Wenger et al. 2011; Crozier and Hutchings 2014; Kovach et al. 2016). The goal of this study was to highlight the increase in individual energetic cost associated with a warming climate as a mechanism regulating in part the size and structure of local populations of juvenile steelhead in their natal streams. Water temperature is an important factor which influences individual performance and population dynamics in the studied population (Myrvold and Kennedy 2015a, b, d), and we hence expected that further increases in water temperature due to climate change can be important. Predicting a future situation based on a single variable can be speculative, however, as other changes may occur simultaneously (Beer and Anderson 2013). For example, it can be expected that climatic change will also result in altered streamflow, changes in stochastic events, and shifts in stream productivity and community structure (Isaak et al. 2010; Wenger et al. 2011; Al-Chokhachy et al. 2013), all with the potential to modulate the effects of greater metabolic demands associated with elevated water temperatures. Nevertheless, metabolic demands scale directly and predictably with water temperature in fishes (Brett 1971; Hewett and Kraft 1993; Hanson et al. 1997; Brown et al. 2004), and it is thus likely that a warming trend will result in elevated individual energetic demands (Rijnsdorp et al. 2009). The extent to which this is ultimately manifested in population size will depend on concurrent changes in the stream ecosystem (Wenger et al. 2011; Al-Chokhachy et al. 2013; Beer and Anderson 2013) as well as plastic and adaptive shifts in the life-history expression of steelhead (Benjamin et al. 2013; Kendall et al. 2015; Phillis et al. 2015). This article concerns the energetic consequences of warming water temperatures during a period of the summer when rearing steelhead experience the highest water temperatures of the year.

The predicted temperature increase was relatively uniform across the watershed (average 1.8°C by the 2040s), as the area we considered is relatively small compared to the scale at which the warming trend is expected to affect the region (Mote and Salathe 2010). However, because of the temperature gradient and local heterogeneity within the watershed, the percent increase varied considerably among the study sites. Relatively cooler sites were predicted to experience the highest proportional increases in temperature, whereas relatively warmer sites had a smaller proportional increase. Because the proportional temperature increase was larger, and because the inflection point in the relationship between temperature and maintenance consumption rate was approximately at 18°C, the increases in energetic cost were also higher in the cooler sites. Importantly, the proportional increase in energetic cost exceeded that of the increase in temperature in these sites due to the nonlinear relationship between these variables in the parameter range experienced by fish in this system, where August mean temperatures ranged from 15.1°C to 19.3°C (Figures 3 and 5). The currently cooler sites were predicted to approach the current temperatures observed in the warmer sites. These reaches are located within a similar physiographic setting, and the shape of the current size distributions of juvenile steelhead across this temperature gradient may therefore be used to inform the future state under a warming trend.

In discussing how increases in energetic cost can be manifested in population numbers it is necessary to also consider the structure of the population. Most populations of plants and animals exhibit skewed size distributions. Pfister and Stevens (2002) proposed that asymmetric competition (resource acquisition, growth, and survival) is the most important mechanism responsible for generating size variability within cohorts, i.e. when individuals experience the same conditions. Asymmetric competition can be detected by studying individual growth performance over time (Lomnicki 1999; Pfister and Stevens 2002). If resources are distributed unevenly among individuals in a consistent manner, size disparities are thought to increase over time (a pattern known as growth autocorrelation), but more often, trade-offs between the ability to acquire resources and avoid risk can change throughout ontogeny. In other words, growth and survival on the long term depend on other factors than momentary size alone. Larger size might therefore not always confer a growth advantage, which is why initially small individuals could experience growth compensation at a later stage (Pfister and Stevens 2002).

In heterogeneous environments, abiotic factors interact with density dependence to influence individual performance (Buckley et al. 2010; Crozier et al. 2010; Myrvold and Kennedy 2015a). The impact of environmental factors can be detected when individuals from multiple populations are followed simultaneously (Myrvold and Kennedy 2015b). Myrvold and Kennedy (*in press*) studied size – growth relationships in the same steelhead population. They found a positive correlation between an individual's relative size and its growth rate (i.e. larger individuals grew faster), but importantly, this relationship was context dependent: during periods of high water temperatures and in relatively warmer streams reaches the positive effect of a relatively large body size diminished. This finding indicates that abiotic conditions can exert an important control over biotic interactions and individual performance (Crozier et al. 2010).

Several studies have investigated the genetic and behavioural causes of individual variation and asymmetric competition. There can be considerable variation in metabolic rate among individuals within a population, and the expression of these traits vary depending on the context. A commonly observed pattern in juvenile salmonids is the correlation between aggressive behaviour and growth rate whereby aggressive individuals can better compete for resources (Abbott and Dill 1989; Nakano 1995). However, if the supply of prey is dynamic in space and time, the selection for these traits can be counterbalanced by the relatively higher energetic cost of such behaviour (Vøllestad and Quinn 2003; Biro and Stamps 2010; Robertsen et al. 2014; Sloat and Reeves 2014). Sloat and Reeves (2014) experimentally tested how the spatial predictability of food influenced behaviour and demography in juvenile steelhead in artificial channels. When food availability was predictable, there was a positive selection for individuals exhibiting a high standard metabolic rate, and conversely, a negative directional selection for this trait under low food predictability. These energetic controls are likely to be stronger with increasing temperatures (Hewett and Kraft 1993), which suggests that temperature can act as an important mediator of the profitability of aggression in wild populations. Our study did not investigate the individual-level basis for size disparities in the population, but merely focused on documenting the shape variation in size distributions; however, we note that as the body of literature which examines the genetic and behavioural basis for individual variation in aggression and behaviour is growing, it becomes increasingly clear that the patterns of social interactions and competition are complex and context-dependent (Millidine et al. 2009; Reid et al. 2012, Adriaenssens and Johnsson 2013; Sloat and Reeves 2014).

Comparing the shapes of the size distributions in multiple local populations allowed us to simultaneously quantify the effects of temperature and density on the size variation in local cohorts. Although the local populations are located within a relatively small watershed, they experience a range of abiotic conditions and exist at varying densities (Myrvold and Kennedy 2015d). Few studies have compared the shape variation of fish cohorts in space or time, but Ohlberger et al. (2013) investigated the shape variation in European perch (*Perca fluviatilis*) in Lake Windermere, United Kingdom. Factors both extrinsic and intrinsic to the population explained the variation in the skewness of cohort size distributions. Notably, food availability related positively to the skewness of the size distributions. Temperature related positively to mean length in the perch and decreased distribution skewness, presumably due to concurrent eutrophication in the lake (Ohlberger et al. 2013). Connolly and Brenkman (2008) examined size distributions in rainbow trout in the Elwha River, Washington, both upstream and downstream of a dam. They could not discern whether the overall smaller sizes in the lower section owed to higher density, less food due to disrupted flows, or some combination of the factors (Connolly and Brenkman 2008). However, the water temperatures were also higher downstream of the dam. Energetic demands in concert with competition likely contributed strongly to the smaller overall size in the lower section.

The variation in size distribution skewness across the gradients of density and temperature hence suggests that individual size might be influenced by temperature in addition to competition. The negative skewness in the warmer sites indicates that most individuals were able to meet their resource demands due to low densities, but that high temperatures may create an upper size threshold above which the absolute energetic demands become too great (Myrvold and Kennedy 2015b). Although mass-specific energetic demands decrease with fish mass, the absolute demands increase (Myrvold and Kennedy 2015b). We therefore hypothesize that the direct effects of temperature were more important than competition in limiting the size of the largest fish in the relatively warmer sites, and conversely, that asymmetric competition was more important in the cooler, denser sites where dominance hierarchies were established and a few dominant individuals could competitively displace their conspecifics (Figure 6). This hypothesis is supported by Myrvold and Kennedy (*in press*) who demonstrated how temperature can modulate the outcome of asymmetric competition, and by Crozier et al. (2010) who documented that the average size of juvenile Chinook salmon was positively related to water temperature at low population densities, but negatively related to temperature at high population densities.

Could the observed patterns be used to predict the future abundance and size distribution in reaches across the watershed? In absence of a proportional increase in food availability, fewer individuals can be supported by the environment because of elevated metabolic demands. This would likely be manifested in increased emigration- and mortality rates, depressed growth opportunities for individuals, and an altered size distribution (Nakano 1995; Keeley 2001; Einum et al. 2011; Hartson and Kennedy 2015; Myrvold and Kennedy 2015a). Because study reach characteristics (stream order, physical habitat and biotic communities) were relatively similar across the temperature range (Myrvold and Kennedy 2015a, d), we expect that the abundance and size distribution in the currently cool sites will approach those of the currently warmer sites, i.e. a flatter and wider size distribution that is slightly negatively skewed. The effects on currently warmer sites are more difficult to elucidate beyond that of energetics, because the predicted temperatures lie beyond the parameter space we have yet observed. In addition to direct energetic effects, future conditions in these sites could see altered community structure, habitat configuration, and water quality, with potentially important consequences for rearing steelhead (Hicks et al. 1991; Tinus and Reeves 2001; Waples et al. 2009; Reed et al. 2011; Benjamin et al. 2013). Important to note is that the density of subyearlings may ultimately depend on the distribution and abundance of adult spawners (Einum et al. 2011) so that higher initial densities occur closer to spawning grounds.

Could the greater energetic demands be compensated by increased food availability, e.g. through increased production of aquatic invertebrates? From a strictly caloric perspective, increased consumption could compensate for higher temperature-induced metabolic costs, everything else being equal. However, the relationship between consumption and food availability is more complex, and depend on concurrent shifts in the physical environment and the biota (Boughton et al. 2007; McCarthy et al. 2009; Benjamin et al. 2013). For example, streamflows are predicted to decrease due to climate change in the Inland Northwest (Mote et al. 2003; Mote and Salathe 2010). On one hand, this might increase the ability of the fish to detect drifting prey (Hughes and Dill 1990), but on the other hand, fewer prey items might enter the drift in response to lower flows (Harvey et al. 2006). Taxonomic shifts in the invertebrate community might further influence the amount and type of prey in the drift. In other words, predicting changes to the food resources in the face of climatic change and, in turn, how this will affect consumption rates is largely tentative.

Plastic and adaptive changes, as well as behavioral adjustments, can also buffer the population size against climate change (Crozier and Hutchings 2014). Due to their wide distribution, *O. mykiss* exhibits considerable diversity and plasticity in life-history expression and habitat use, which permit the species to persist across a wide range of environments (Sogard et al. 2012; Moore et al. 2014; Kendall et al.

2015). For example, the number of life-history types present in a given watershed reflects an adaptation to the prevailing environmental regimes (Sogard et al. 2012; Kendall et al. 2015), and because these expressions can be dynamic it ensures resilience at the population level (Moore et al. 2014). Given examples from other systems (Benjamin et al. 2013; Moore et al. 2014) and the large adaptive potential in *O. mykiss*, we expect both plastic and adaptive shifts in response to an altered selection pressure with climate change in the Lapwai Creek watershed (Crozier and Hutchings 2014; Sloat and Reeves 2014; Kendall et al. 2015).

In summary, our findings can help unravel how climate change can manifest in fish populations, and more fundamentally, how abiotic factors can exacerbate demographic density dependence. Future studies should consider concurrent changes to streamflow and productivity as these are often strongly associated with temperature in running waters (Beer and Anderson 2013; Kovach et al. 2016). For example, could increases in stream productivity compensate for increased metabolic demands and less habitat? Climate change will likely lead to altered temperature regimes throughout the entire year. For example, winter temperatures might increase and provide better growing conditions (Sogard et al. 2012) but increased levels of stress associated with ice movement and other hydraulic shifts might offset these thermal advantages. An interesting avenue for future research is to quantify the energetic consequences of changes to the flow and temperature regimes in different environmental settings (Thompson and Beauchamp 2016). Finally, it would be interesting to quantify the variation in expression of behavioural and physiological traits across the range of temperature regimes (Biro and Stamps 2010; Reid et al. 2012; Adriaenssens and Johnsson 2013). This would provide important insights into the operation of selective forces which could prove increasingly important under rapid environmental change, particularly in populations which periodically experience stressful abiotic conditions (Rijnsdorp et al. 2009; Crozier and Hutchings 2014).

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Tables

Table 1. Temperature (°C) predictions for the month of August under the A1B scenario (“balanced scenario”; IPCC 2000) for the study sites in the Lapwai Creek watershed, ID. The table shows, from left, the elevation (m) of the study site and August discharge (m^3/s), the projected current and future temperatures (Isaak et al. 2010), field data measured at each study site and the difference from the predicted temperature, and the corrected predictions for 2040 and 2080 (right panel).

	Physical site characteristics		Projected mean August temperature (°C)			Field data 2010-2012 (°C)		Corrected mean August temperature (°C)			% increase from current	
Site	Elevation (m)	Discharge (m^3s^{-1})	Current	2040	2080	Measured	Correction	Current	2040	2080	2040	2080
LLL	280	0.37	18.27	20.12	21.45	18.41	0.14	18.41	20.26	21.59	10.0	17.3
LLU	324	0.25	18.63	20.49	21.83	18.14	-0.49	18.14	20.00	21.34	10.3	17.6
LSX	390	0.26	17.40	19.21	20.51	17.24	-0.16	17.24	19.05	20.35	10.5	18.0
MLX	357	0.13	18.70	20.57	21.91	19.15	0.45	19.15	21.02	22.36	9.80	16.8

ULL	449	0.053	17.47	19.29	20.59	17.02	-0.45	17.02	18.84	20.14	10.7	18.3
ULM	585	0.054	17.33	19.14	20.44	17.62	0.29	17.62	19.43	20.73	10.3	17.7
ULU	693	0.058	17.03	18.82	20.12	16.62	-0.41	16.62	18.41	19.71	10.8	18.6
UML	411	0.067	17.92	19.75	21.08	19.29	1.37	19.29	21.12	22.45	9.50	16.4
UMM	472	0.053	17.71	19.54	20.85	18.55	0.84	18.55	20.38	21.69	9.90	16.9
UMU	629	0.034	16.73	18.51	19.80	16.57	-0.16	16.57	18.35	19.64	10.7	18.5
USL	448	0.18	16.73	18.52	19.81	16.52	-0.21	16.52	18.31	19.60	10.8	18.6
USM	531	0.13	15.77	17.52	18.78	15.62	-0.15	15.62	17.37	18.63	11.2	19.3
USU	575	0.14	15.07	16.79	18.03	15.11	0.04	15.11	16.83	18.07	11.4	19.6
UWL	438	0.10	17.63	19.45	20.77	17.38	-0.25	17.38	19.20	20.52	10.5	18.1
UWM	490	0.10	17.54	19.36	20.67	16.84	-0.70	16.84	18.66	19.97	10.8	18.6

UWU	525	0.11	16.83	18.62	19.91	16.27	-0.56	16.27	18.06	19.35	11.0	18.9
Average	475	0.13	17.30	19.11	20.41	17.31	-0.026	17.27	19.08	20.38	10.5	18.1
St.dev.	112	0.09	0.92	0.96	0.99	1.16	0.51	1.13	1.16	1.18		

Table 2

Table 2. Candidate models to explain variation in skewness in size distributions of subyearling steelhead. Also shown is the empty model. *Density* refers to the estimated number of subyearlings at a sampling visit (no. per m^2); *biomass* refers to the biomass of subyearlings encountered at a sampling visit (g/m^2); *temperature* refers to the average monthly temperature (°C) in a study site, and *avg. mass* refers to the average subyearling mass (g) during the sampling visit. Shown in parentheses behind each variable is the direction of its influence on the skewness of the distribution. Bolded *AICc* values indicate the best approximating models.

Model	Predictor variable(s)	Random term	*K*	*AICc*	Random effects P(*Z*)	
					Intercept	Residual
0	No predictors (empty model)	intercept	3	88.5	0.045	<0.0001
1	Density (+)	intercept	4	89.0	0.057	<0.0001
2	Biomass (+)	intercept	4	**86.5**	0.066	<0.0001
3	Temperature (-)	intercept	4	89.8	0.039	<0.0001
4	Avg. mass (+)	intercept	4	89.8	0.042	<0.0001
5	Density (+), Temperature (-)	intercept	5	89.7	0.043	<0.0001
6	Biomass (+), Temperature (-)	intercept	5	**88.2**	0.057	<0.0001

7	Avg. mass (+), Temperature (-)	intercept	5	91.7	0.039	<0.0001
8	Density (+), Avg. mass (+), Temperature (-)	intercept	6	90.8	0.052	<0.0001
9	Biomass (+), Avg. mass (+), Temperature (-)	intercept	6	90.5	0.061	<0.0001

Table 3

Table 3. Estimated energetic demand for maintenance metabolism ($J \cdot g^{-1} \cdot d^{-1}$) for different sizes of juvenile steelhead in the study sites under the current temperature regime (2011) and future temperature regime (2040 and 2080) for the month of August. The columns to the right refer to the change in energetic demands for a 10g steelhead from the current situation to the future regimes.

	2.5g			5g			10g			20g			40g			80g			% chg.	
Site	‘11	‘40	‘80	‘11	‘40	‘80	‘11	‘40	‘80	‘11	‘40	‘80	‘11	‘40	‘80	‘11	‘40	‘80	‘40	‘80
LLL	289	316	327	249	271	281	214	234	242	184	201	208	159	173	179	136	149	154	9	13
LLU	285	312	326	245	269	280	211	231	241	182	199	208	156	171	179	134	147	154	10	14
LSX	270	299	317	232	257	272	200	221	234	172	191	202	148	164	173	127	141	149	11	17
MLX	301	323	329	259	278	283	223	239	243	192	206	209	165	177	180	142	152	155	7	9
ULL	266	296	314	229	255	270	197	219	233	170	189	200	146	162	172	126	140	148	11	18
ULM	276	305	321	238	262	276	205	225	237	176	194	204	152	167	176	130	144	151	10	16
ULU	260	289	309	223	249	265	192	214	228	165	184	197	142	159	169	123	136	145	11	19
UML	303	324	329	260	279	283	224	240	243	193	207	209	166	178	180	143	153	155	7	9
UMM	292	317	328	251	273	282	216	235	243	186	202	209	160	174	179	138	150	154	9	12

UMU	259	288	308	223	248	265	192	213	228	165	184	196	142	158	169	122	136	145	11	19
USL	258	288	307	222	248	264	191	213	227	164	183	196	141	158	168	122	136	145	11	19
USM	243	272	293	209	234	252	180	202	217	155	173	187	133	149	161	114	128	138	12	21
USU	234	263	284	201	226	244	173	195	210	149	168	181	128	144	156	110	124	134	12	21
UWL	272	301	318	234	259	274	202	223	236	173	192	203	149	165	175	129	142	150	11	17
UWM	263	293	312	227	252	268	195	217	231	168	187	199	144	161	171	124	138	147	11	18
UWU	254	284	304	218	244	261	188	210	225	162	181	193	139	156	166	120	134	143	12	20
Avg.	270	298	314	233	257	270	200	221	232	172	190	200	148	163	172	128	141	148	10	16
% chg.		10	16		10	16		10	16		10	16		10	16		10	16		

Table 4

Table 4. Calculated maintenance ration (i.e. standard metabolism only) for the actual size distribution of juvenile steelhead in the coolest (USU), average (ULL), and warmest (UML) study site for the month of August under the current and future temperature regimes. The ration is given as total prey biomass over the month based on a prey energy density of 4324 J/g prey (Myrvold and Kennedy 2015b).

				Ration (g prey in August)					
Site	Age class	Abundance	Biomass current (g)	Current	2040	2080	% increase to 2040	% increase to 2080	Temperature rank
USU	Total	**61**	1092	1026	1153	1244	12.4	21.2	Coolest
	Subyearling	39	118	189	213	229	12.4	21.3	
	Yearling	22	975	837	941	1014	12.4	21.2	
ULL	Total	**59**	352	552	613	651	11.1	17.9	Average
	Subyearling	59	352	552	613	651	11.1	17.9	
	Yearling	0	0	-	-	-	-	-	
UML	Total	**55**	659	915	980	993	7.1	8.5	Warmest
	Subyearling	47	256	465	497	504	7.1	8.5	

	Yearling	8	403	451	483	489	7.1	8.6
All sites		**175**	2103	2493	2747	2888	10.2	15.8

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Table 5

Table 5. Summary statistics for the subyearling size distributions for the month of August. CV refers to the coefficient of variation.

Site	Area (m^2)	Abundance	Avg. mass (g)	Median mass (g)	SD mass (g)	CV	Biomass (g/m^2)	Skewness	Kurtosis	Range
LLL	747	20	16.7	15.1	7.5	44.6	0.55	0.29	-1.25	23.1
LLU	677	53	12.2	11.1	3.8	30.8	1.1	0.89	1.06	18.3
MLX	624	31	9.6	9.1	2.8	29.5	0.49	1.27	2.49	13.6
ULL	482	59	7.9	7.7	2.8	35.7	0.78	0.79	0.98	13.2
ULM	439	101	4.3	4.2	1.3	30.2	1.1	0.99	1.65	8.1
ULU	551	146	4.5	4.3	1.5	33.6	1.2	0.28	-0.35	7.5
UML	478	47	7.8	8.1	3.8	48.9	0.34	0.99	1.30	14.9
UMM	438	106	5.4	5.0	1.9	36.1	1.4	1.20	2.74	11.2
UMU	363	29	3.8	3.8	0.8	21.0	0.33	0.20	-0.27	3.1
USL	311	18	10.8	10.9	3.0	27.5	0.73	-0.24	-0.41	10.3
USM	390	13	8.2	8.4	2.0	24.2	0.32	0.00	-1.19	6.3
USU	395	39	4.5	4.3	1.4	31.9	0.74	0.46	0.30	6.8
UWL	286	10	2.2	2.2	0.3	13.7	0.16	-0.32	0.20	1.0
UWM	370	80	4.3	4.0	1.3	31.5	0.96	0.84	0.01	5.9
UWU	353	63	3.2	2.9	1.1	33.5	0.63	0.74	0.02	4.9

Table 6

Table 6. Parameter estimates for the variance components model and the best approximating models for skewness in the size distribution of subyearling steelhead. Standard errors are given in parentheses. ρ(unconditional) refers to the proportion of variance attributable to the two levels (site and visit), and ρ(unconditional) refers to the proportion of the variance explained by the covariates in the model.

Model and variables	Parameter estimate (SE)	ρ(unconditional)	ρ(conditional)
Variance components (0)			
Intercept γ_{00}	0.617 (0.092)		
Random intercept (site) τ_{00}	0.0786 (0.046)	30%	
Residual (visit) σ^2	0.183 (0.039)	70%	
Best model (2, *w*=0.38)			10.3%
Intercept γ_{00}	0.408 (0.13)		
Biomass γ_{10}	0.316 (0.15)		
Random intercept τ_{00}	0.0563 (0.037)		28.4%
Residual σ^2	0.179 (0.038)		2.6%
Second best model (6, *w*=0.16)			10.1%
Intercept γ_{00}	0.706 (0.356)		

Biomass γ_{10}	0.306 (0.153)	
Temperature γ_{20}	-0.0197 (0.022)	
Random intercept τ_{00}	0.0628 (0.0398)	20.0%
Residual σ^2	0.173 (0.0366)	5.8%

Figures

Figure 1

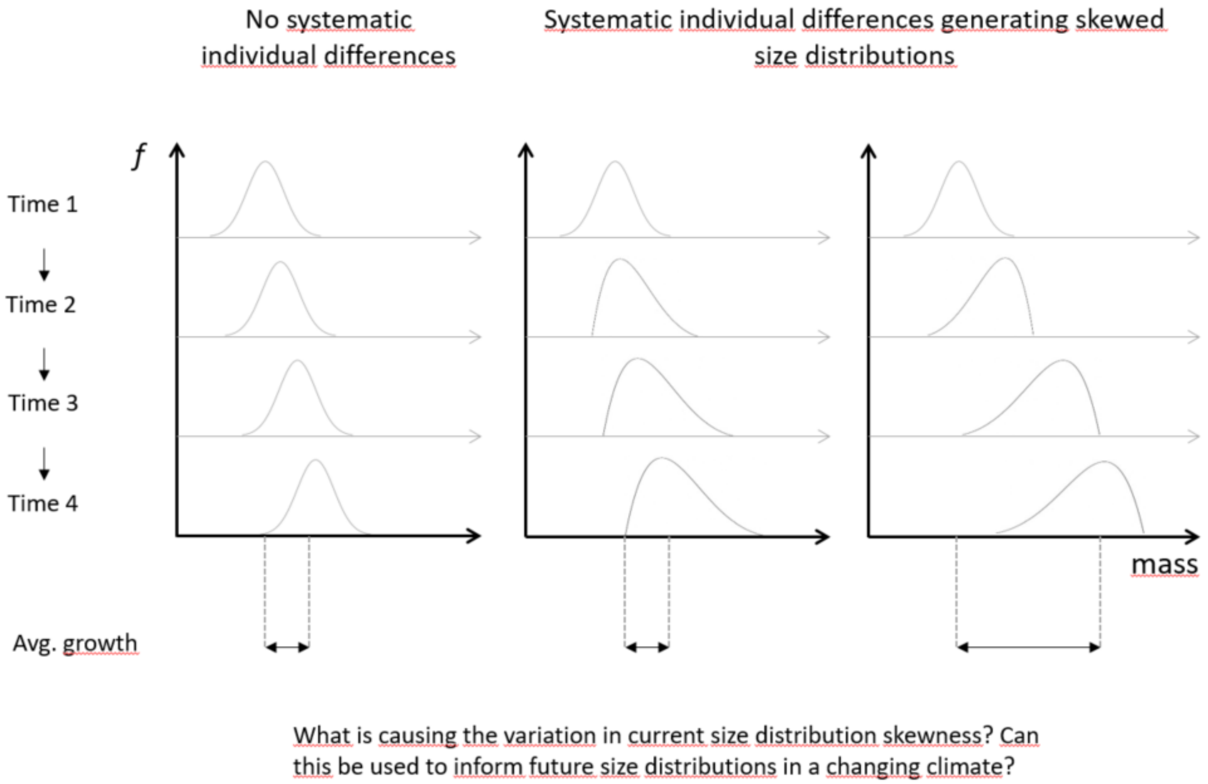

Figure 1. Conceptual figure showing the size distributions of juvenile steelhead in a single cohort at four time points. The left panel shows a situation with no systematic individual differences, whereas the middle and right panels show systematic individual differences, which generate skewed size distributions. While the pattern depicted in the left panel may represent random variation in individual growth rates over time, the middle panel shows a situation with asymmetric competition. Here, a few individuals capture most of the resources and grow amply, whereas the average individuals in the

cohort grow less. In the right panel there is less competition for the available resources, and most individuals can grow fast. Here, the direct constraints of the environment may pose an upper limit to the size of the largest individuals. This study aimed at identifying the factors that generate skewed size distributions in present day in order to predict the potential shifts associated with climate change.

Figure 2

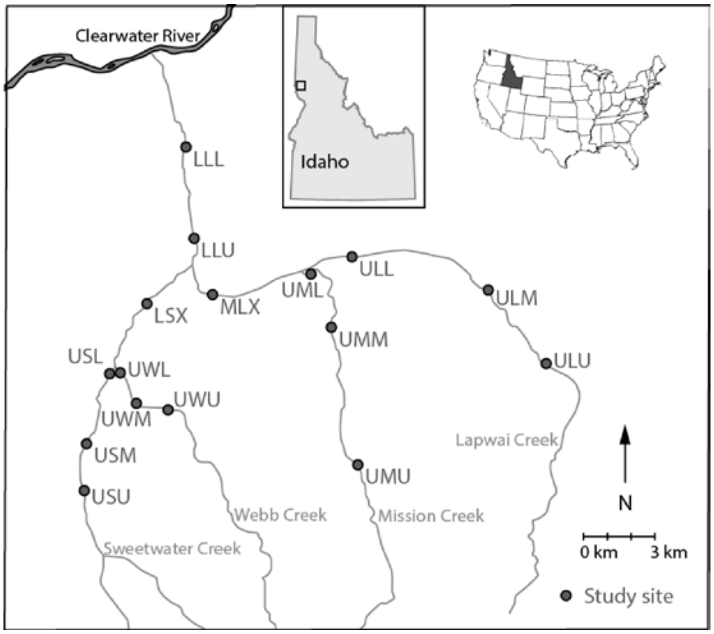

Figure 2. Map of the study watershed (center at 46°17’N, 116°44’W) and its location in Idaho, United States (inset). Modified from map data provided by DigitalGlobe, Inc., Westminster, Colorado, USA.

Figure 3

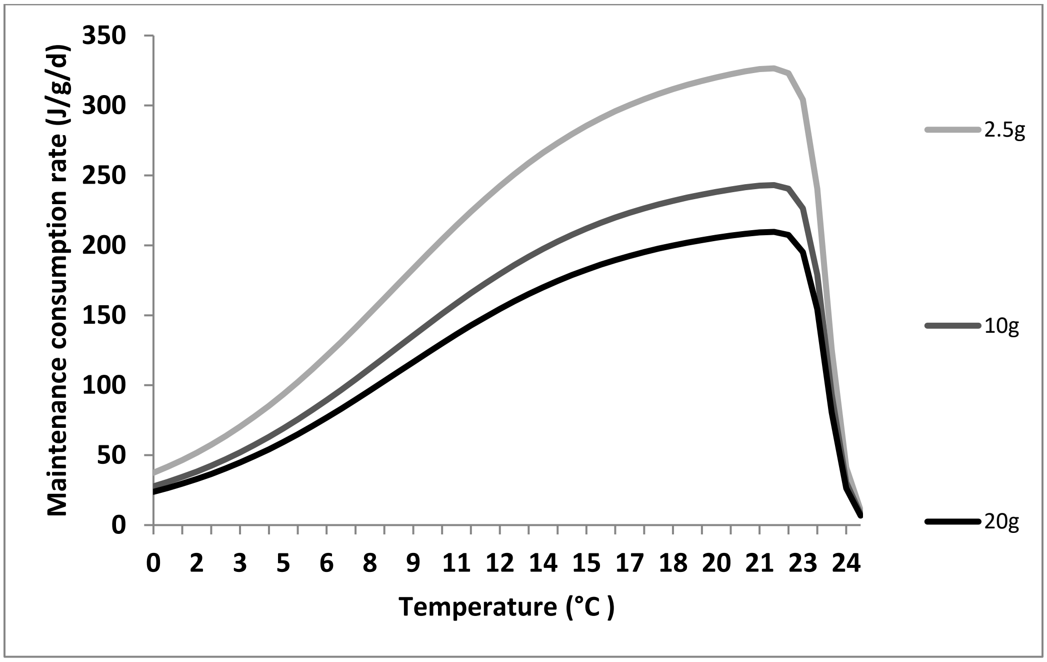

Figure 3. Daily mass-specific consumption rates (J·g^{-1}·d^{-1}) necessary to maintain standard metabolism as a function of temperature for three sizes of juvenile steelhead.

Figure 4

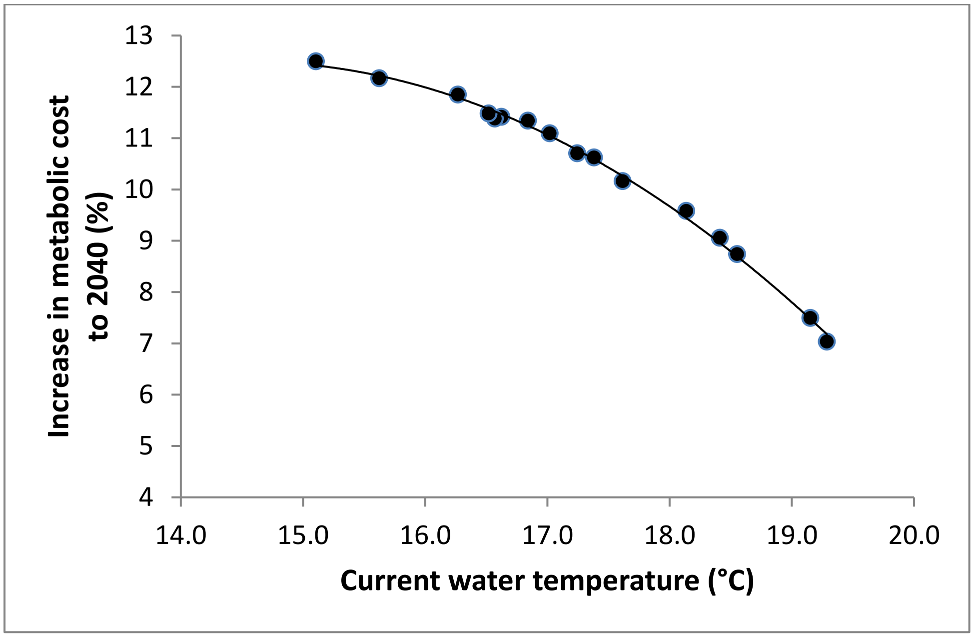

Figure 4. Predicted increase in maintenance metabolic cost (%) to the 2040s as a function of current temperature (°C) for a 10g juvenile steelhead in the 16 study sites in the Lapwai Creek watershed. The equation for the second-order polynomial regression is $y = -0.236x^2 + 6.87x - 37.5$.

Figure 5

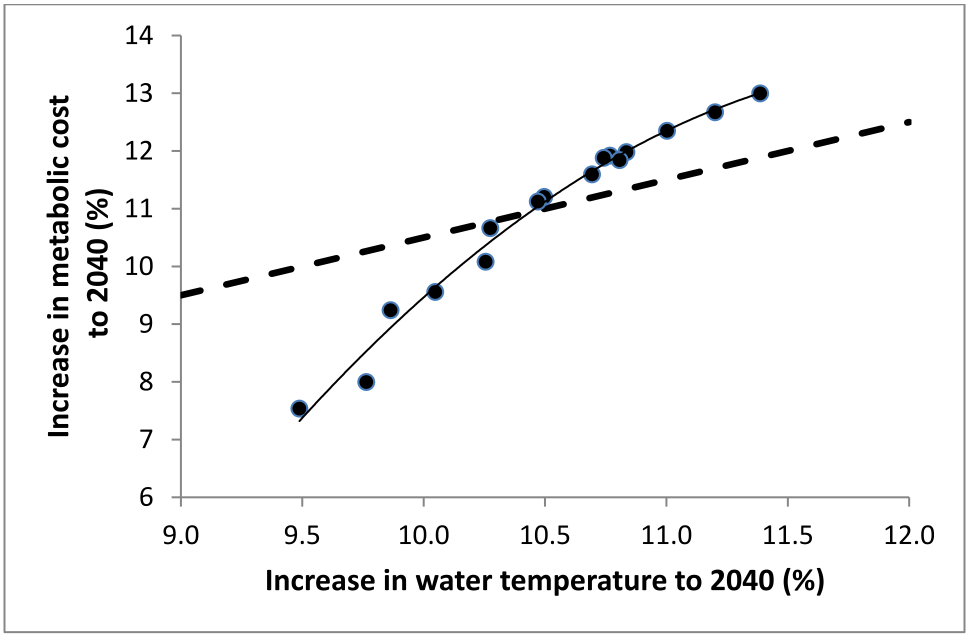

Figure 5. Relationship between the predicted increase in temperatures (%) to 2040 in each of the 16 study sites and the associated predicted increase in energetic cost (%) for a 10g juvenile steelhead. Dashed line indicates 1:1. Differential increases owe to the nonlinear relationship between maintenance consumption rate and temperature in the 15.0°C to 19.5°C region, which is why a certain increase in water temperature does not yield a similar increase in energetic cost. The equation for the second-order polynomial is $y = -0.86X^2 + 21.1x - 115$.

Figure 6

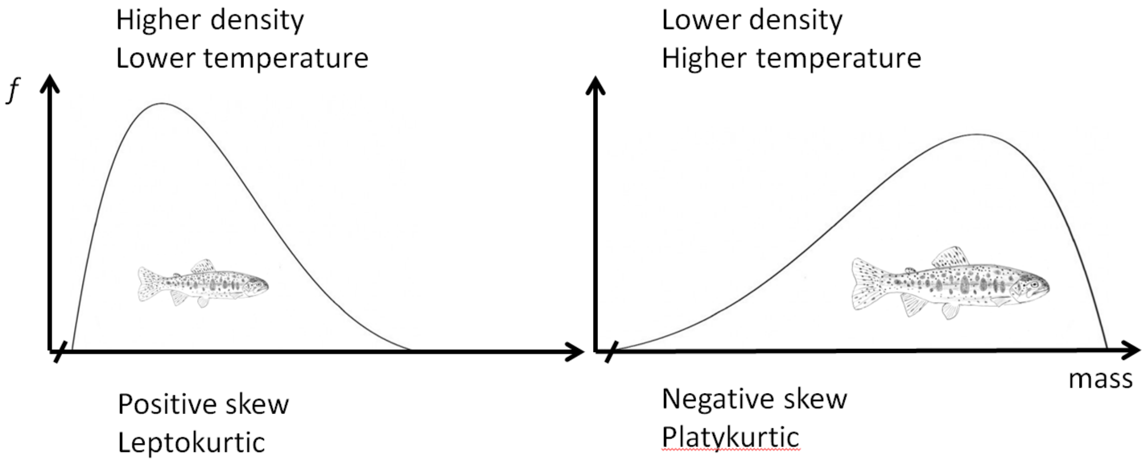

Figure 6. Conceptual figure showing size distributions of subyearling steelhead. Sites with high densities and low temperatures were positively skewed (left), whereas sites with low abundances and high temperatures were negatively skewed (right). With a warming trend due to climate change, we hypothesize that currently positively skewed populations will approach a negatively skewed size distribution.